

**RESPONSES IN THE HABITAT OCCUPANCY,  
MOVEMENT BEHAVIOR, AND WING MORPHOLOGY  
OF TWO SPECIES OF CALOPTERYGID DAMSELFLIES  
TO LANDSCAPE STRUCTURE**

by

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## Abstract

I examine the responses of two species of damselfly, *Calopteryx maculata* and *Calopteryx aequabilis*, to differences in landscape structure. I performed surveys to determine patterns of stream occupancy in relation to habitat characteristics measured at small spatial scales, and the medium-scale characteristic of distance to forest. I show that the relative importance of these habitat characteristics differs among species and between survey years. The changes over time are consistent with weather patterns.

I then examine the relative abilities of these two species to move through forest and pasture landscapes. Previous work had suggested that *C. maculata* uses forest as a resource more consistently than *C. aequabilis*. Results from manipulative experiments show that the connectivity of pasture landscapes is higher than forest landscapes for *C. maculata*. There was no detectable difference in connectivities for *C. aequabilis*. These results have implications regarding the relative propensities of individuals to disperse within the structurally different landscapes.

I examine the wing morphologies of *C. maculata* and *C. aequabilis* individuals collected from landscapes of differing structure. I show that the fore and hindwings of *C. maculata* individuals are consistent in their asymmetric distributions (left - right) across landscapes. The forewings of *C. aequabilis* individuals inhabiting a highly fragmented landscape exhibited a significantly higher degree of asymmetry, and were significantly shorter overall, than those inhabiting a moderately fragmented landscape. Forewings of female *C. maculata* individuals collected from high connectivity (pasture) landscapes were slightly longer than those from low connectivity (forest) landscapes.

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## **General Introduction**

I present in this thesis the results of explorations into how the occupancy of reproductive habitat, the movement capabilities, and the wing morphologies of two species of damselfly - *Calopteryx maculata* and *Calopteryx aequabilis* - are related to landscape structure. I conducted these assessments in a region where the two species co-exist, and exhibit both *intraspecific* and *interspecific* behavioral variability in response to the spatial separation of two focal resources - streams (reproductive habitat) and forest (foraging habitat). My methods draw upon these variant behaviors to help derive a mechanistic understanding of the relationships between landscape structure and the particular individual responses that I measure.

### **Animal - landscape structure interactions**

Landscape structure refers to the amount, composition, and configuration of resources within a landscape (Dunning *et al.*, 1992), and also considers the ease with which a given animal moves among those resources within a given landscape (Taylor *et al.*, 1993). This latter component, termed "landscape connectivity" (Merriam, 1984), integrates the former more static features of the landscape with dynamic attributes of individual animals, such as behavior (Merriam, 1991). In this sense, landscape structure is an organism-defined concept (Kareiva, 1987; Wiens *et al.*, 1993; Ims, 1995).

The interactions of individual animals with landscape structure underlie fundamental ecological patterns and processes such as animal distribution, population dynamics, and in many ways - evolution (e.g. Andrewartha and Birch, 1984; Cappucino, 1995; McPeck, 1995). In particular, animal movement is a behavior that gives rise to the distributions we observe, and mediates the dynamics therein (Kareiva, 1990; Wiens *et al.*, 1993). That animals are not always distributed in a manner consistent with the distribution of their

resources is of fundamental importance in ecology (Wiens *et al.*, 1993). To explain the differences ecologists draw upon theory that attempts to account for behavior (e.g. optimal foraging theory; Krebs *et al.*, 1983), demography (e.g. density-dependence; Turchin, 1995), or some aspect of both (reviewed in Kareiva, 1990).

At broad spatial scales, however, behavioral data is scarce (Lima and Zolner, 1996), and ecologists are forced to make certain assumptions about the information available to the animals (Lima and Zolner, 1996), and the movement behaviors of the animals (Kareiva, 1990). One consequence has been that ecological theory at these scales emphasizes the static components of landscape structure (e.g. landscape indices; assessed in Schumaker, 1996), sometimes in conjunction with demographics (e.g. metapopulation theory; Hanski and Gilpin, 1991), but almost exclusively in isolation of individual behavior and its variability (but see Turner *et al.*, 1993). In general, it is assumed that organisms respond in a linear fashion to landscape structure, and do so within the confines of uniform exogenous (e.g. interspecific interactions, weather) or endogenous (e.g. age, or levels of parasitism) conditions (Kareiva, 1990).

Several examples from the field highlight this as a potentially serious shortcoming.

### **Evidence for complex animal - landscape structure interactions**

Fahrig and Paloheimo (1987) demonstrate in their single-species system that the spatial resolution at which individual female cabbage butterflies perceive and respond to the distribution of host plants depends on the time required for egg production. Thus, the realized isolation of habitat patches was primarily a function of the dispersal behavior of the individual butterflies (i.e. their mean daily displacement) interacting with the physiological process of egg production. Ims *et al.* (1993) showed that different genetic strains of the root vole (one aggressive, one docile) responded to habitat fragmentation in

considerably different ways with respect to home-range establishment. While being consistent with the levels of aggressiveness, the responses were sex-dependent: the home ranges of docile females, and those of both docile and aggressive males overlapped considerably in the remnant habitat fragments, while aggressive females established non-overlapping territories. These are examples of how endogenous factors influence animal interactions with landscape structure.

Multi-species interactions provide examples of exogenous factors that influence animal - structure relationships. Kareiva (1987) demonstrated that habitat fragmentation promoted outbreaks of a prey species (aphids), because of reduced efficiency in the search behavior of their primary predators (ladybirds). Roland and Taylor (1997) later demonstrated similar relationships, at larger spatial scales, involving forest-tent caterpillars and four species of parasitic flies. They show that parasitism is significantly reduced or enhanced depending on the proportion of forested to unforested land. They also show that each parasitoid responds to fragmentation at a different spatial scale, corresponding to their relative body sizes.

Another form of exogenous factor, particularly relevant to ectotherm systems, is that of micro-climate. For example, Bach (1984) found that sunlight levels significantly affected the movement behaviors, patch choice, and residency times of *Acalymma* beetles within variously structured locales. When given the choice, the beetles consistently chose host plants within the sun. At broader spatial and temporal scales, Solbreck (1995) found that the year-to-year dynamics of a lygaeid bug (*Lygaeus equestris*) system can be adequately described through the interactions of weather, host plant density, and bug movement behavior. There were direct effects of weather on the insect (flight behavior and large-scale extinction due to severe weather), and indirect effects through food density (seed production is related to weather).

An example of "non-linear" interactions of animals with landscape structure is

provided by Wiens *et al.* (1997), who observed that beetle movement within a particular cell (0.25m) in their experimental mosaic was contingent on the structure of the greater surrounding (micro)landscape (5 x 5m). In this case the structure of the greater surrounding landscape is an exogenous influence of sorts.

### **An experimental approach**

The above examples demonstrate how, in our attempts to obtain a more thorough understanding of animal - landscape structure relationships, we might benefit from the explicit consideration of individual behavior (Hassel and May, 1985), and its variability in relation to both spatial scale (Ims *et al.*, 1993; Wiens *et al.*, 1993), and exogenous and endogenous factors (Kareiva, 1990; Solbreck, 1995).

Beyond their obvious merits, I chose to use these particular examples because they share certain attributes. First, each examines their respective process of interest at *an appropriate, organism-defined spatial scale* - from the scale of metres (Kareiva, 1987) to hundreds of metres (Roland and Taylor, 1997). This "appropriate scale" is largely defined by the movement behavior of the subject organism(s). In experiments where this was not considered explicitly (or otherwise unknown), only a limited amount of information could be gleaned (e.g. Kruess and Tschardtke, 1994; Dempster *et al.*, 1995). Second, these examples represent a spectrum of experimental approaches: from manipulation of both individuals and habitat (Ims *et al.*, 1993), to manipulation of individuals only (Fahrig and Paloheimo, 1987), and finally manipulation of habitat only (Kareiva, 1987; Roland and Taylor, 1997). Third, each example exploits some key behavioral (differentials in movement capabilities) or life history attribute (oviposition period, Fahrig and Paloheimo, 1987) in its design, and takes account of possible endogenous (Ims *et al.*, 1993) or exogenous (Bach, 1984; Solbreck, 1995) sources of variation. Equally important is that each draws upon a solid understanding of the behavioral ecology of their respective

systems (Ives, 1995; Lima and Zolner, 1996).

In this thesis I too explore the benefits to these approaches in trying to better understand the various responses of individual animals to landscape structure. I use a model system of two congeneric species of damselfly - *Calopteryx maculata* and *Calopteryx aequabilis* - that are similar in all but a few aspects of their natural histories. Both species inhabit streams as naiads and adults, and the adults mate and oviposit where there is oviposition material (emergent aquatic vegetation). Each species uses forest as a foraging resource to some degree, but *C. maculata* more consistently than *C. aequabilis*. The key feature of this system is the patchy distribution of reproductive and foraging resources (forest), and in particular, the way in which individuals of both species respond to that patchiness in their foraging (movement) behavior. In continuous forest landscapes the two resources are adjacent, and damselflies need not move far to access them. In moderately fragmented landscapes forest is separated from stream habitat by distances up to 500m. In these landscapes some individuals of both species continue to access forest patches by making directed flights through the intervening (non-resource) matrix. This behavior is observed more frequently in *C. maculata* individuals than in *C. aequabilis* individuals. In highly fragmented landscapes where forest is further than 500m from stream habitat, individuals of both species appear to remain at the stream throughout the day, and evidently do not use forest as a resource.

I use this variation in behavior as a type of treatment within experiments designed to measure various responses of individual damselflies to landscape structure.



I compare the following responses of individual *C. maculata* and *C. aequabilis* to differences in landscape structure.

1) **Habitat occupancy:** I present the results of surveys, conducted over two summers, that quantify the relative importance of various small-scale habitat characteristics, and the larger scale property of distance to forest, to stream occupancy by *C. maculata* and *C. aequabilis*. Considerable differences in weather between the years served to highlight how exogenous factors can constrain behavior, and perhaps habitat "quality". These results build upon previous work regarding the behavioral ecology of the two species in this region, and serve to clarify some of the more subtle differences in their natural histories.

2) **Movement behavior:** Based upon observations made in Chapter 1, I make predictions concerning the connectivity of pasture and forest landscapes for these two species of damselfly. I describe the results of manipulative experiments designed to directly measure the relative abilities of each species to move through the two kinds of structurally dissimilar landscapes, over spatial scales relevant to their population dynamics in this region.

3) **Morphology:** I first test whether patterns of fluctuating asymmetry in the wings of the two species correlate in some way with differences in landscape structure. I also test whether wing size is consistent with the behavioral plasticity observed among individuals inhabiting forest and pasture landscapes. Specifically, I test whether the wings of individuals inhabiting moderately fragmented landscapes are larger than those of individuals inhabiting continuous forest landscapes.

**Chapter 1. Stream occupancy by *Calopteryx maculata* and *Calopteryx aequabilis* is related to habitat characteristics measured at two spatial scales.**

**Introduction**

Organisms respond to the structural attributes of their surroundings across a range of spatial scales (Senft *et al.*, 1987; Wiens, 1989; Lima and Zolner, 1996). Those responses depend on the processes being carried out (e.g. migration versus oviposition), and are constrained by endogenous factors (e.g. mobility, Cain *et al.*, 1985; Ims, 1995) and exogenous factors (e.g. weather, Solbreck, 1995; habitat persistence, Denno *et al.*, 1996). Responses to structure at a given spatial scale may be affected by processes acting at broader scales (e.g. total amount of habitat, Wiens *et al.*, 1997), or at finer scales (e.g. Roland and Taylor, 1997). Determining the relative importance of scale-specific attributes and processes to organisms and their systems is a fundamental goal in ecology (Turner *et al.*, 1989). Determining how those values change in response to endogenous and exogenous factors is key to understanding the long-term dynamics of those systems (e.g. Solbreck, 1995).

*Calopteryx maculata* and *Calopteryx aequabilis* (Odonata: Calopterygidae) are relatively large damselflies that are widespread in eastern North America (Walker, 1953; Waage, 1975), and sympatric throughout my study region of the Annapolis Valley, Nova Scotia (Meek and Herman, 1990). They inhabit streams as nymphs, and reproduce along streams as adults (Johnson, 1962; Henderson and Herman, 1984). Males are territorial at oviposition resources (emergent aquatic vegetation), and exhibit resource-defense polygyny (Alcock, 1987; but see Forsyth and Montgomerie, 1987). Experiments have shown that adults perceive and respond to the amount, quality, and dispersion of oviposition resources along the stream (Alcock, 1987; Waage, 1987; Meek and Herman, 1990a; Gibbons and Pain, 1992). Subtle differences exist in those responses between the species, and adult distributions at these fine spatial scales (i.e. metres) reflect those

differences (Meek and Herman, 1990a). Complex mating behaviors (described in detail by: Johnson, 1962; Waage, 1975; Conrad and Herman, 1987; Meek and Herman, 1990b), in conjunction with consensual attraction in females, further contribute to the distributional patterns observed at these fine spatial scales (Alcock, 1987; Waage, 1987; Meek and Herman, 1990a). Other factors may include the location of oviposition material with respect to perch sites, vegetation cover, or amounts of shade (Waage, 1987).

Their behaviors away from stream suggest that both species perceive habitat features at medium spatial scales also (i.e. tens of metres to several hundred metres). For example, forest serves as potential foraging and roosting habitat for both species (Waage, 1972; pers. obs), and provides shelter for maturing teneral (Waage, 1972). When forest is separated from their reproductive habitat by 200-500 m, *C. maculata* individuals link the two resources by making directed flights through the intervening non-resource (pasture) matrix (Taylor and Merriam, 1995). One consequence is that, on average, individuals in fragmented pasture landscapes are distributed over a greater distance away from the stream than individuals inhabiting forested landscapes (Taylor, 1993). I have observed a few *C. aequabilis* individuals making similar directed flights, though not as consistently, nor over as much distance. When they occur within landscapes where forest is scarce (i.e. > ca. 500 m from streams), both species appear to remain at the stream throughout the day, and evidently do not use forest as a resource.

It has been suggested that *C. maculata* generally prefers small, shaded streams with intermittent rapids (Robert, 1963), while *C. aequabilis* occurs primarily along larger, slower, more open streams and rivers (Martin, 1939; Walker, 1953). Waage (1975) noted no consistent habitat segregation between the two species through casual observations at locations throughout eastern North America.

I was interested in determining the relative importance of various reproductive habitat characteristics (i.e. fine scale features) and the availability of forest (i.e. medium scale

feature) to stream occupancy by *C. maculata* and *C. aequabilis*. I show that the relative importance of these habitat characteristics differs among species, and that it changes from one flight season to the next. These changes are consistent with weather conditions. I also show that although it is considered primarily a forest damselfly (Johnson, 1962; Forsyth and Montgomerie, 1987), *C. maculata* occurs at a similar proportion of sites across a range of forest proximities.

### **Study Area**

The Annapolis Valley in Nova Scotia (45°05'N; 64°30'W) is a large (roughly 1800km<sup>2</sup>) mosaic of farmland and variously sized woodlots, sheltered by forested hills to the north and south. Abutting the Bay of Fundy the northern hills are considerably cooler than the rest of the region, and both the pH and the water temperature of the streams were lower there than in the valley proper and the southern hills (June 1996 data) (mean  $\pm$  s.d.: north hills pH (n = 23) 6.85  $\pm$  0.45; valley and southern hills (n = 59) 7.52  $\pm$  0.78; north hills water temperature (n = 23) 10.51  $\pm$  1.78; valley and southern hills (n = 35) 15.72  $\pm$  3.24; for both, Wilcoxon rank sum test  $p < 0.01$ ). Preliminary surveys determined that Calopterygid damselflies did not occur there. Both the eastern and western ends of the valley drain watersheds through tidal dykelands. It is the watersheds of the southern hills and valley that provide suitable reproductive habitat for *C. maculata* and *C. aequabilis*, and thus the general study area for my research.

### **Methods**

Local habitat characteristics (Table 1-1) and damselfly numbers were assessed along 50m transects, at five 10m intervals, established along 48 randomly chosen streams in 1995, and 33 in 1996. With a few exceptions, two transects were used per stream, giving 87 sample sites for 1995, and 58 for 1996. I refined the surveys in 1996 to include only

streams that supported some form of aquatic vegetation. Due to logistical constraints, most transects were situated near easy access points (e.g. trails and bridges), but they were always established at least 10m from human-made structures. All transects were also situated at least 1km apart to minimize the possibility of recounts within a day. Seven minute counts of damselflies were performed at each transect. Surveys were each conducted over a period of 2-3 days during fair-weather ( $> 24^{\circ}\text{C}$ , sunny), between 1000h and 1700h. With the help of one other observer, three surveys were performed each summer, one in each of the months June, July, and August.

Air photos (1:10000) and field observations were used to assign the survey sites to one of three categories of FOREST<sup>1</sup> proximity:  $<50\text{m}$ ,  $50\text{-}500\text{m}$ ,  $>500\text{m}$ . These categories were chosen based on observations of daily inter-resource movements of each species (Taylor and Merriam, 1995). "Forest" is defined here as a forest patch large enough to provide light gaps that often serve as foraging locales for damselflies (Taylor and Merriam, 1995). Thus the riparian woods (e.g. alder) that provide shade at some streams do not classify as forest, nor do orchards. A site was considered positive for presence if a damselfly was observed in any of the three surveys (for each respective year). For each species and each year I analyze site occupancy (presence or absence) using logistic regression, with the four local habitat characteristics (Table 1-1), and the medium scale characteristic of distance to FOREST, as independent explanatory variables. For a given model, each explanatory term was manually dropped from the full model and the resulting change in deviance was assessed against the appropriate critical chi-square value. Terms contributing more than the critical value in deviance were retained. Because of slight co-linearity between the variables SUN and FOREST, I always fit SUN first in the model, restricting my assessment of FOREST to that of variance explained over and above that explained by SUN. In this respect I was limited in my ability to interpret directly the

<sup>1</sup> Throughout the thesis, factor names included in statistical models are in SMALL CAPS font.

relative importance of each variable, however graphical representations elucidate trends. The goodness-of-fit of each model was assessed using residual diagnostics (McCullagh and Nelder, 1989). All statistical models presented were fit using the *glm* procedure in Splus (Chambers and Hastie, 1992).

The remaining local habitat variables, stream pH and temperature (sampled only in 1996), were assessed separately due to lack of independence among pairs of sites common to one stream. I randomly discarded one site from each stream that originally supported two sampling transects. In this way I could proceed with univariate tests to compare pH values and temperatures among unoccupied sites and sites occupied by either *C. aequabilis* or *C. maculata*. The resulting sample sizes were  $n = 44$  for pH, and  $n = 26$  for water temperature.

I also acquired weather data recorded at the Kentville Agricultural Research Station, in Kentville, Nova Scotia. The weather station is situated near the centre of my study region. For each of the months of May-July in each year, the mean daily maximum temperatures, total monthly rainfall, and the number of sunlight hours per month were noted.

## Results

I first note the weather conditions of each survey period (Table 1-2). The spring of 1995 was particularly warm and dry compared to the spring of 1996, and consequently streams were drier earlier in the season. Several heavy rainfalls during each of the summer months of 1996 kept streams relatively deep. The summer of 1996 was cool compared to the summer of 1995, and there were considerably fewer sunlight hours.

### *Site occupancy*

*C. aequabilis* occurred at more survey sites than *C. maculata* in both years (Table 1-3). Proportionately more sites supported damselfies in 1996 than in 1995. This is likely

attributable to my refined sampling methods (I did not survey sites lacking aquatic vegetation of some sort).

*Small-scale habitat characteristics:*

The goodness-of-fit of the logistic regression models varied among years and species. For both years the *C. maculata* models had dispersion parameters near 1 (1995: residual degrees of freedom (RDF) = 84, residual deviance (RD) = 77; 1996: RDF = 56, RD = 52), but they fit poorly over some ranges of the data. For *C. aequabilis*, the models fit quite well over most of the data. In the 1995 model, there is some evidence of "over-fitting" (1995: RDF = 81, RD = 49; 1996: RDF = 53, RD = 54). Overall, the models adhere to assumptions relatively well, so I proceed with their interpretation with the aid of appropriate figures. Note that the order of inclusion of each factor did not affect their overall significance in the models.

In agreement with weather conditions, the likelihood of site occupancy increased for both species with increasing DEPTH in 1995 (Table 1-4). Because some sites support both species, direct comparisons of DEPTH among species was not possible. Figure 1-1, however, indicates that *C. aequabilis* inhabits only slightly deeper streams than *C. maculata* (as indicated by shaded 95% confidence intervals). In 1996 DEPTH was not a significant variable for *C. maculata*, and only slightly so for *C. aequabilis* (Table 1-4). Although significant for both species in 1995 (Table 1-4, Figure 1-2), ovIP did not contribute significantly to the models in 1996 (Table 1-4). This was likely due to my change in methodology in 1996 - only surveying sites that had some form of aquatic vegetation. In both years *C. aequabilis* was more likely to occur at sites within the "high" category of SUN (Tables 1-3 and 1-4), and in 1995 it tended to be present over a smaller range of FLOW rates than did *C. maculata* (Figure 1-3). In 1996 only the SUN variable was significant in explaining occupancy for *C. maculata* (Table 1-4), and FLOW was similar

among occupied and unoccupied sites (Figure 1-3). Again these patterns are consistent with weather conditions.

Water temperatures and pH for sites located on unique streams (i.e. only one transect per stream) are shown in Figure 1-4. Water temperatures were significantly higher at *C. aequabilis* sites than at unoccupied sites (Wilcoxon signed rank test:  $Z = 2.05$ ,  $p < 0.05$ ; sample sizes  $n = 12$  and  $n = 12$  respectively), and slightly higher at *C. maculata* sites compared to unoccupied sites ( $Z = 1.73$ ,  $0.05 < p < 0.10$ ; sample sizes  $n = 7$  and  $n = 12$  respectively). I found no significant differences in pH between sites occupied by *C. aequabilis* and unoccupied sites ( $t = 1.56$ , d.f. = 42,  $p > 0.10$ ), nor between *C. maculata* sites and unoccupied sites ( $t = -1.33$ , d.f. = 42,  $p > 0.10$ ).

#### *Distance to forest and amount of sunlight*

Distance to FOREST explained a significant amount of variation in site occupancy over and above the amount of SUN in both 1995 and 1996 for *C. aequabilis*. It was not a significant factor in the *C. maculata* models. Tables 1-6 and 1-7 show site occupancy for each species, respectively, according to distance to forest and category of SUN. With the exception of one site in 1995, *C. aequabilis* occurred only at sites where forest was further than 50m away (Table 1-5, Figure 1-5). *C. maculata* was present at a similar proportion of sites within all three categories of distance to forest (Table 1-6, Figure 1-5). Irrespective of the distance to forest, both species occurred more frequently at sites of "high" categories of SUN. In the one case where *C. aequabilis* was observed at a forested stream, the sampling transect was open to the sunlight (Figure 1-6). In both years *C. aequabilis* does occur at sites of "low" category of SUN, but only in the middle category of distance to FOREST (Figure 1-6). In 1995 *C. maculata* was found in good proportions at both shaded and sunny sites where forest was within 50m (Figure 1-7). In the cooler summer of 1996 I observed *C. maculata* only at forested survey sites more open to



sunlight (Figure 1-7).

## **Discussion**

Determining the relative importance of scale-specific attributes and processes to organisms and their systems is a goal fundamental to ecology (Turner *et al.*, 1989). Assessing patterns of habitat occupancy through space and time can provide some answers in this regard, and also provide insight as to how exogenous factors such as weather influence those systems (Solbreck, 1995). I examined the patterns of stream occupancy of two congeneric species of damselfly, *Calopteryx maculata* and *C. aequabilis*, to highlight how interactions between organisms and their environment are scale-dependent, and how exogenous factors such as weather can moderate those interactions.

I first demonstrate in the 1995 surveys that both species inhabit streams only where oviposition resources are available (Table 1-4; Figure 1-2). I therefore excluded streams in the 1996 surveys that could not support aquatic vegetation because of their substrate (i.e. gravel and rock with no signs of vegetation). I also show that streams occupied by *C. maculata* and *C. aequabilis* in 1996 are warmer than unoccupied streams (Figure 1-4). Optimum rearing temperatures for naiads of these species is thought to be near 18-19°C (Martin, 1939). The sites occupied by both species have water temperatures nearer these values than do unoccupied sites (Figure 1-4).

With respect to other small-scale habitat characteristics, it has been suggested that *C. maculata* generally prefers small, shaded streams with intermittent rapids (Robert, 1963), while *C. aequabilis* occurs primarily along larger, slower, more open streams and rivers (Martin, 1939; Walker, 1953). I demonstrate quantitatively (in agreement to what Waage (1975) suggests through anecdotal observations) that depth and flow are not consistent discriminatory factors governing stream occupancy *between* the two species. The depth

of streams occupied by *C. maculata* were similar to those occupied by *C. aequabilis* (Figure 1-1) in both years. However, depth is likely an important factor governing stream occupancy by both species in general, especially under the effects of dry weather. In 1995 the spring was warmer and drier than in 1996, and streams were likely shallower overall. There were several heavy rainfalls in 1996 that kept stream levels relatively high. I found that in 1995 DEPTH was a significant factor governing site occupancy by both species, but in 1996 only for *C. aequabilis* - and then only marginally so (Tables 1-4, 1-5). *C. aequabilis* did tend to occupy slightly slower streams overall than *C. maculata* (Figure 1-3), but this was not significant (Tables 1-4 and 1-5). In general, both species preferred sites that were open to sunlight (even though I only surveyed on high ambient temperature days) (Figures 1-6 and 1-7), but *C. maculata* was found at more shaded sites overall (Tables 1-6 through 1-9). The inconsistencies between the years, however, revealed how the shade-tolerance of *C. maculata* is possibly constrained by the exogenous factor of weather. In the cooler year of 1996 *C. maculata* did not occur at forested streams where sites were primarily shaded, whereas in 1995 they occurred at 4 such sites (Tables 1-6 and 1-7). This type of direct effect that weather has is a feature of many ectotherm systems (e.g. Kindvall *et al.*, 1995). For example, Bach (1984) found that sunlight levels significantly affected the movement behaviors, patch choice, and residency times of *Acalymma* beetles within variously structured locales. When given the choice, the beetles consistently chose host plants within the sun.

The medium-scale feature of distance to FOREST revealed that *C. aequabilis* occupies sites where forest is >50m away more so than *C. maculata* (Figure 1-5). In a way, this supports the suggestion that they prefer more "open" streams (Martin, 1939; Walker, 1953). Of particular interest is that this variable was significant over and above the effect of SUN (Tables 1-4 and 1-5). Considering this with the weather-mediated effect of SUN on *C. maculata*, I suggest that there are two mechanisms responsible for any differences

observed in stream occupancy between these species. First, the small-scale feature of amount of SUN affects each species differently. *C. maculata* tolerates shady sites, but that tolerance is constrained by overall weather conditions. *C. aequabilis*, however, will only occupy shady sites if open areas are nearby, as in the middle and high categories of distance to forest (Figure 1-6). The larger scale feature of distance to forest affects the stream occupancy of *C. aequabilis* over and above the effect of SUN; they are found more frequently at sites where forest is more distant than 50m (Figure 1-5). *C. maculata*, however, is found at sites with a range of forest proximities (Figure 1-5).

The interacting effects that I observe here between weather and stream occupancy could have implications for these species' regional population dynamics. First, both species are only reproductively active during warm weather (Johnson, 1962; Conrad and Herman, 1987). As a direct effect on damselfly behavior, consistently cool weather might limit the opportunities for mating to occur, and thus reduce the recruitment rate in the following year(s) (*C. maculata* naiad development is completed in one year while *C. aequabilis* generally takes two; Martin, 1939; Walker, 1953). An indirect effect of weather on these damselflies is suggested in the pattern of stream occupancy as it relates to stream depth. Sufficiently dry weather could limit the spatial distribution of these damselflies to only those streams that do not run dry. In this regard, the year-to-year "quality" of stream habitat likely changes in response to weather conditions, and thus so too would the spatial distribution of the damselflies. Solbreck (1995) demonstrated similar interactions between weather, habitat, and his study organism - lygaeid bugs. In his broad spatial and temporal scale study he first showed that weather can have direct effects on the animal's movement behavior (Solbreck, 1976), and that summer mortality is negatively correlated with sunshine hours (Solbreck, 1995). Weather indirectly affected the bugs through its limitation of host plant seed production (Solbreck, 1995). In my study system I don't know the specifics of how weather affects the availability of

oviposition material. I would expect that densities are likely positively related to sunshine hours and temperature, but are ultimately limited by water levels. It is interesting to note that in 1996 damselflies remained numerous at two sites (where they are known to be consistently abundant; Annapolis River south of Aylesford; 356000m E; 4987000m N), even though water levels were so consistently high that oviposition material was completely submerged out of sight.

### **Summary**

The results I present here demonstrate how small-scale (measured over metres) and medium-scale (measured over tens to hundreds of metres) characteristics of the landscape are related to the patterns of habitat occupancy of two congeneric species of damselfly - *Calopteryx maculata* and *C. aequabilis*. They also show how one aspect of *C. maculata* behavior - shade tolerance - is possibly constrained by weather. Habitat quality may also be affected by weather through its limitation of stream depth. These effects were revealed through changes in habitat occupancy from one year to the next.

**Table 1-1.** Description of local habitat characteristics assessed in surveys.

Variable	Type	Description
OVIP <sup>†</sup>	pseudo-continuous	Measure of oviposition patch density; Number of 10m intervals with suitable oviposition material (0-5).
SUN <sup>†</sup>	category	Measure of incident sunlight reaching stream; "High" represents 50% or more of transect in sunlight, "Low" represents <50%.
FLOW <sup>†</sup>	pseudo-continuous	Measure of average flow rate; Each interval was assigned a number, 0 representing no flow, 1 for slow, 2 for moderate, and 3 for fast. Rates were classified by eye. The value used in model is the average of the rates, so a transect with 2 moderate and 3 fast flow rates would have a FLOW value of $13/5 = 2.6$ .
DEPTH (cm) <sup>†</sup>	continuous	Measure of stream size; natural logarithm of the average depth of transect, measured to the nearest 5cm.
PH *	continuous	Measured at each site during June surveys using a digital pH meter.
TEMP (°C) **	continuous	Measured at most sites during June surveys using a digital thermometer.

<sup>†</sup> Variables used in logistic regression models.

\* Only measured in 1996 and \*\* only at some sites, and both assessed using graphical methods.

**Table 1-2:** Weather data recorded at, and acquired from the Kentville Agricultural Research Station, Kentville, Nova Scotia.

Weather data	May		June		July	
	1995	1996	1995	1996	1995	1996
Mean max. high (°C)	14.7	13.5	24.1	22.7	25.3	23.7
Total precipitation (mm)	84.0	112.7	103.9	46.2	123.5	160.8
Total sunlight hours (h)	177	165	220.4	211.3	192	176

**Table 1-3.** Site occupancy of *C. maculata* and *C. aequabilis* at 1995 and 1996 survey sites.

Year	Number of survey sites supporting:			Total occupied (%)
	Only <i>C. aequabilis</i> (%)	Only <i>C. maculata</i> (%)	Both species (%)	
1995	13 (14.9)	7 (8.0)	11 (12.6)	31 (35.6)
1996	16 (27.6)	3 (5.2)	8 (13.8)	27 (46.6)

**Table 1-4.** Summary of logistic regression models for 1995 survey data, showing non-significant explanatory terms (ns), and significant terms with their directions of effect. See text for details of analyses.

Term	<i>C. maculata</i>		<i>C. aequabilis</i>	
	Parameter	Significance	Parameter	Significance
	<i>t</i> - value	p ( $\chi^2$ )	<i>t</i> - value	p ( $\chi^2$ )
OVIP	1.76	0.003	2.17	<0.001
SUN	ns	ns	1.99	<0.001
FOREST (cat 1-2) *	ns	ns	2.24	0.070
FOREST (cat 2-3)	ns	ns	-0.03	na
FLOW	ns	ns	ns	ns
DEPTH (m)	1.73	0.07	2.59	0.001

\* FOREST is modeled as an ordered factor, and so parameter estimates correspond to successive changes from one category to the next.

**Table 1-5.** Summary of logistic regression models for 1996 survey data, showing non-significant explanatory terms (ns), and significant terms with their directions of effect. See text for details of analyses.

Term	<i>C. maculata</i>		<i>C. aequabilis</i>	
	Parameter	Significance	Parameter	Significance
	<i>t</i> - value	p ( $\chi^2$ )	<i>t</i> - value	p ( $\chi^2$ )
OVIP	ns	ns	ns	ns
SUN	1.80	0.032	0.80	0.002
FOREST (cat 1-2)	ns	ns	0.57	0.004
FOREST (cat 2-3)	ns	ns	-0.57	na
FLOW	ns	ns	ns	ns
DEPTH (m)	ns	ns	1.91	0.040

**Table 1-6:** Site occupancy of *C. maculata* at 1995 survey sites according to the categories of distance to forest and sun.

SUN category	Distance to forest						Totals
	< 50m		50 - 500m		> 500m		
	Present	Absent	Present	Absent	Present	Absent	
High	2	4	8	24	2	4	44
Low	4	15	2	18	0	4	43
Totals:	6	19	10	42	2	8	87

**Table 1-7:** Site occupancy of *C. maculata* at 1996 survey sites according to the categories of distance to forest and sun.

SUN category	Distance to forest						Totals
	< 50m		50 - 500m		> 500m		
	Present	Absent	Present	Absent	Present	Absent	
High	2	2	7	21	1	5	38
Low	0	9	1	9	0	1	20
Totals:	2	11	8	30	1	6	58

**Table1-8:** Site occupancy of *C. aequabilis* at 1995 survey sites according to the categories of distance to forest and sun.

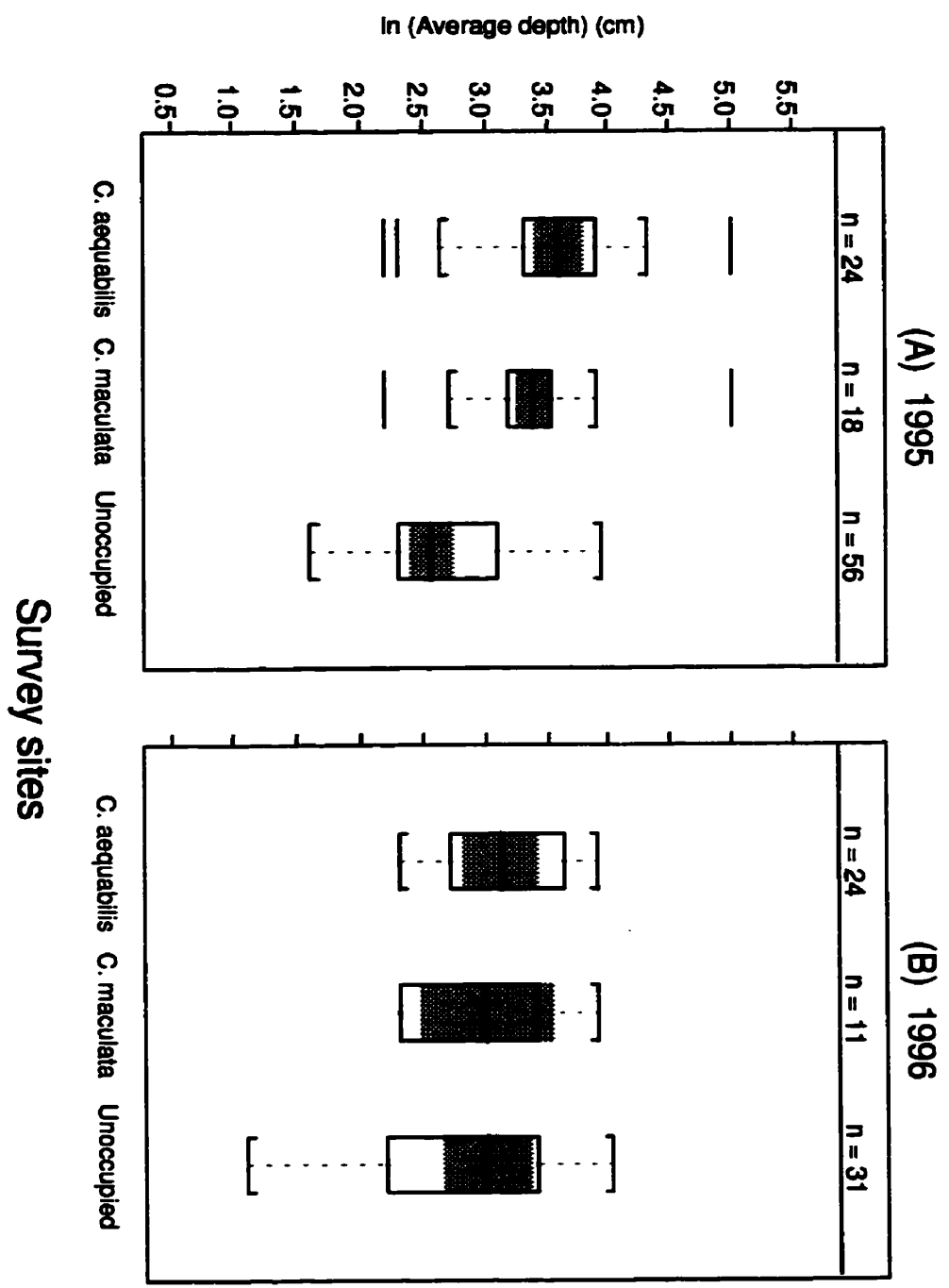
SUN category	Distance to forest						Totals
	< 50m		50 - 500m		> 500m		
	Present	Absent	Present	Absent	Present	Absent	
High	1	5	17	15	4	2	44
Low	0	19	2	18	0	4	43
Totals:	1	24	19	33	4	6	87

**Table1-9:** Site occupancy of *C. aequabilis* at 1996 survey sites according to the categories of distance to forest and sun.

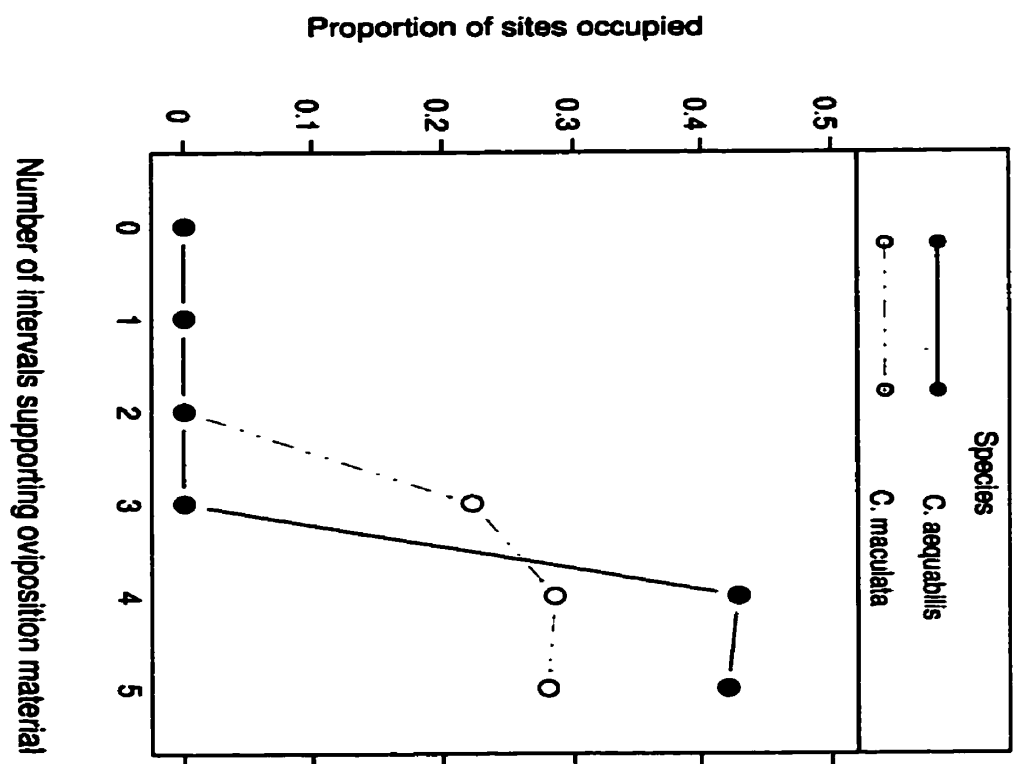
SUN category	Distance to forest						Totals
	< 50m		50 - 500m		> 500m		
	Present	Absent	Present	Absent	Present	Absent	
High	0	4	17	11	4	2	38
Low	0	9	3	7	0	1	20
Totals:	0	13	20	18	4	3	58

**Figure 1-1.** Boxplots showing median (black bar), 95% confidence interval (shaded), interquartile range (box), range (whiskers), and outliers (bars) of the natural logarithm of stream depth at (A) 1995 and (B) 1996 survey sites, grouped by those supporting *C. aequabilis* individuals, *C. maculata* individuals, and no individuals (unoccupied).



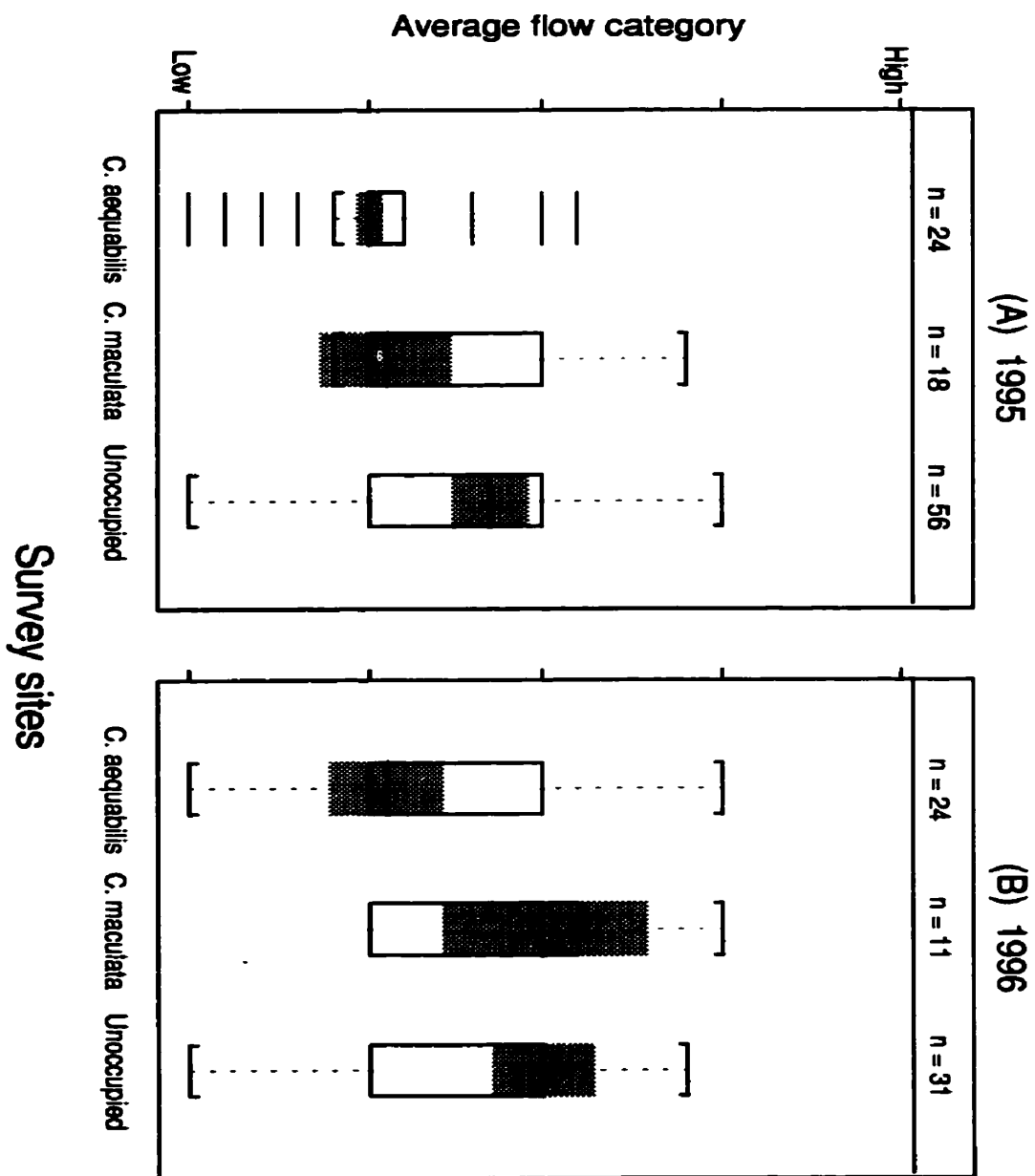


**Figure 1-2.** Interaction plot showing how the proportion of survey sites occupied by *C. maculata* and *C. aequabilis* in 1995 changes with the increasing number of intervals supporting oviposition material (OVP).

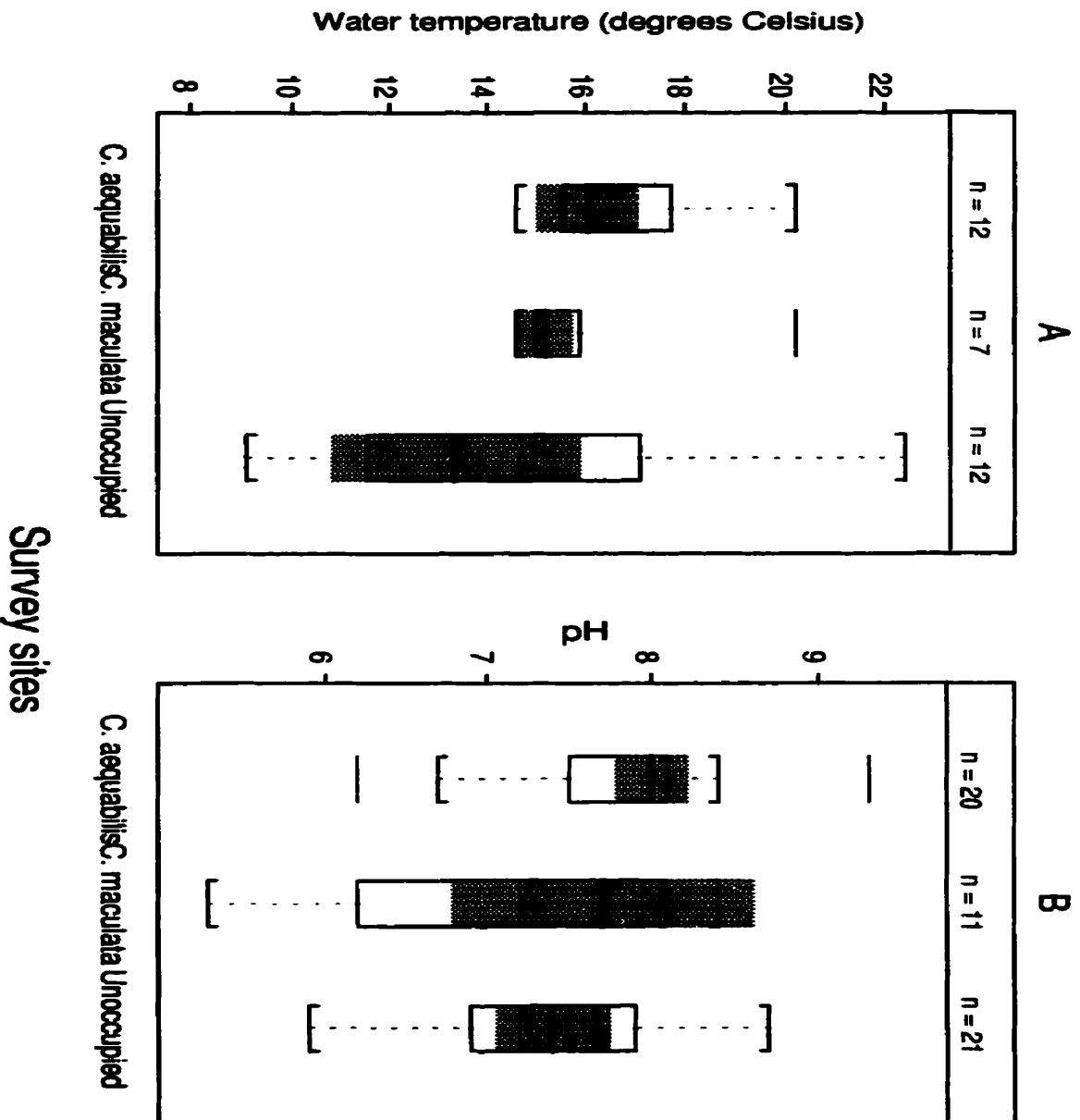


**Figure 1-3.** Boxplots showing median (black bar), 95% confidence interval (shaded), interquartile range (box), range (whiskers), and outliers (bars) of FLOW<sup>1</sup> rate at (A) 1995 and (B) 1996 survey sites, grouped by those supporting *C. aequabilis* individuals, *C. maculata* individuals, and no individuals (unoccupied).

<sup>1</sup> See Table 1-1 for a description of this variable.

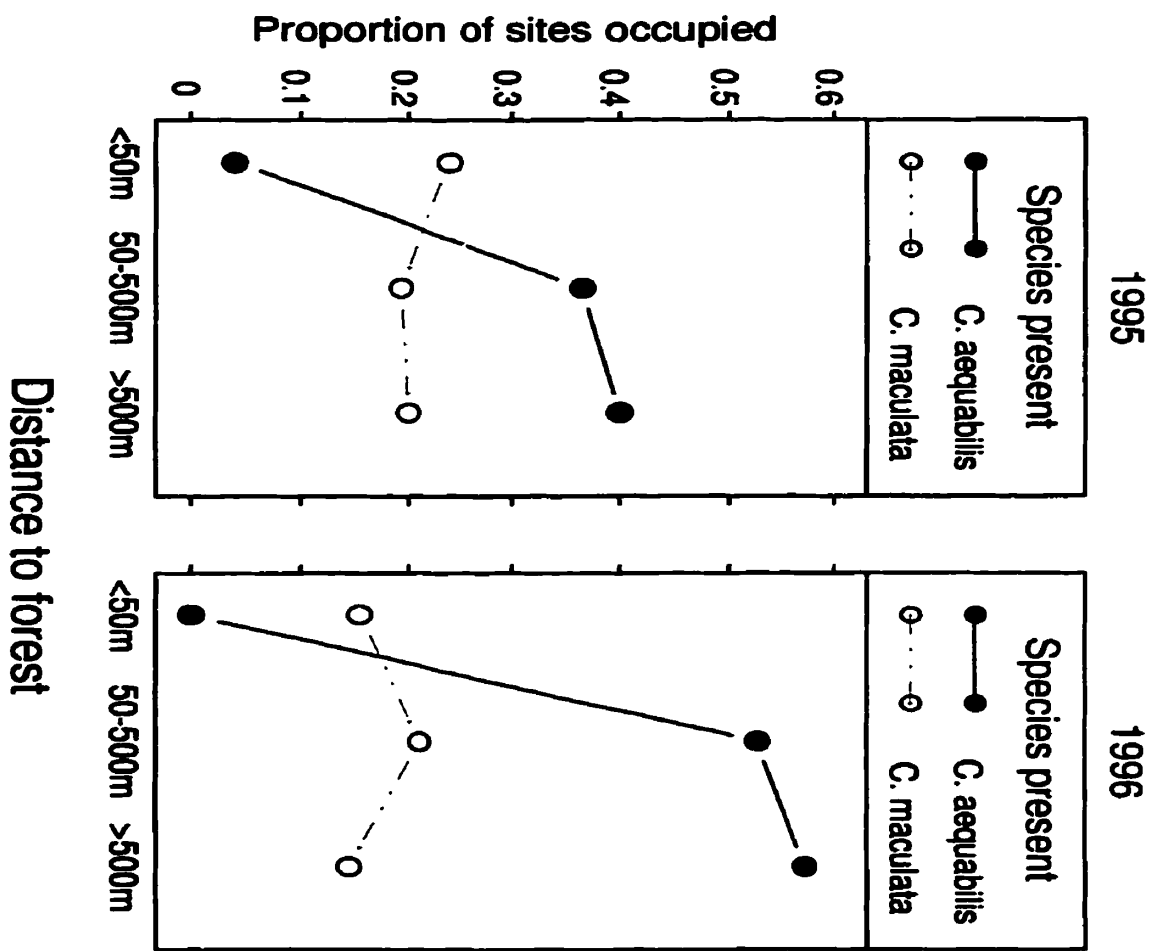


**Figure 1-4.** Boxplots showing median (black bar), 95% confidence interval (shaded), interquartile range (box), range (whiskers), and outliers (bars) of (A) water temperature in °C and (B) pH of 1996 survey sites, grouped by those supporting *C. aequabilis* individuals, *C. maculata* individuals, and no individuals (unoccupied).

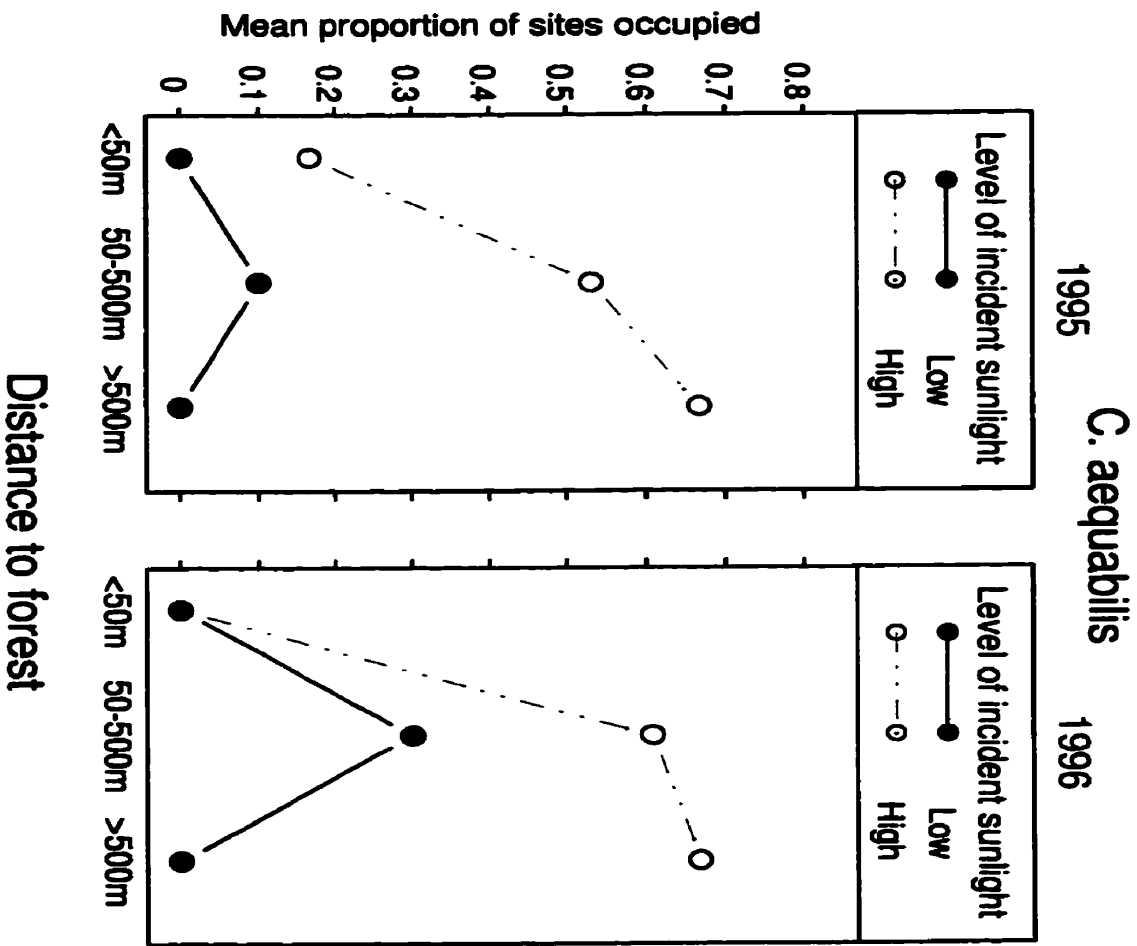


**Figure 1-5.** Interaction plot showing how the proportion of survey sites occupied by *C. maculata* and *C. aequabilis* in (A) 1995 and (B) 1996 changes with the category of distance to forest (FOREST).

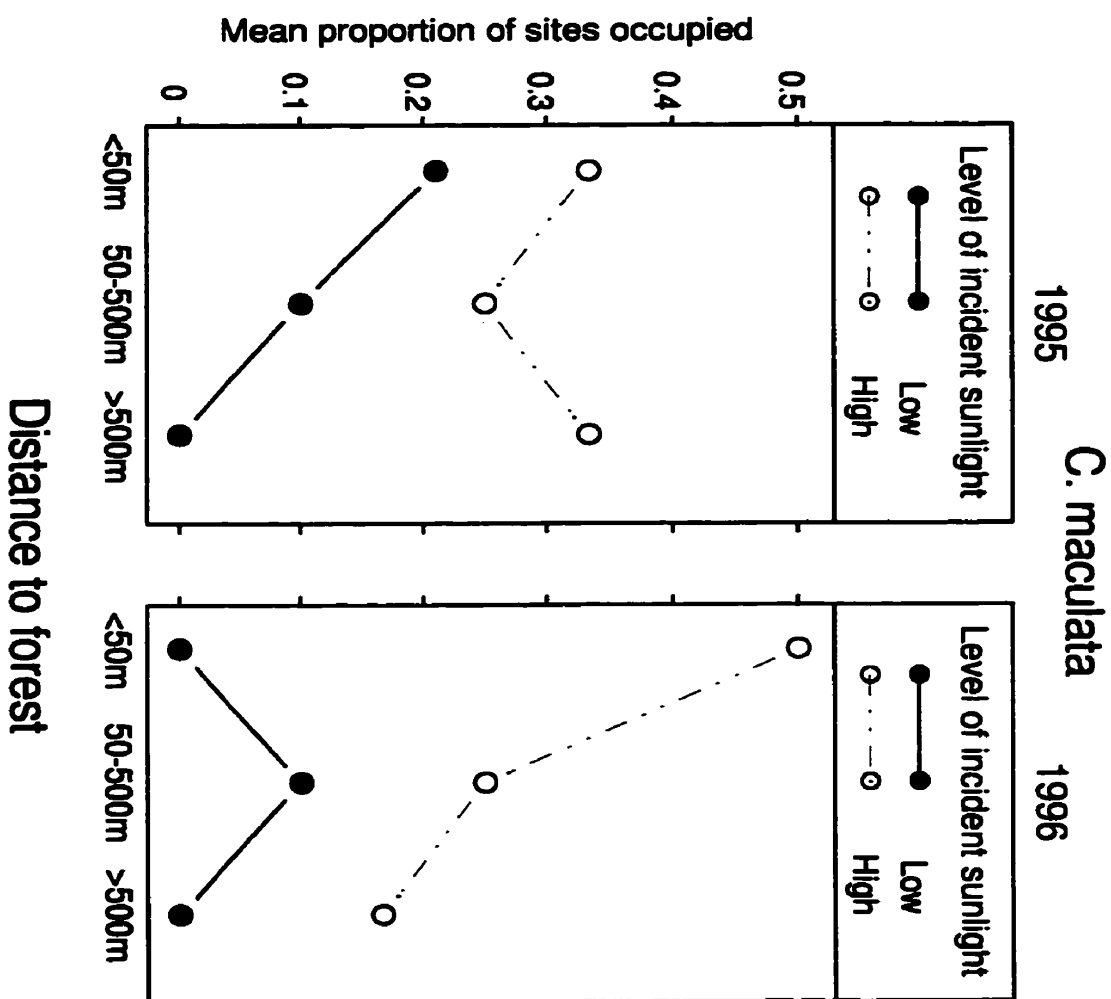




**Figure 1-6.** Interaction plot showing how the proportion of survey sites occupied by *C. aequabilis* in (A) 1995 and (B) 1996 changes with the category of SUN.



**Figure 1-7.** Interaction plot showing how the proportion of survey sites occupied by *C. maculata* in (A) 1995 and (B) 1996 changes with the category of SUN.



## **Chapter 2. An experimental assessment of connectivity in pasture and forest landscapes for *Calopteryx maculata* and *Calopteryx aequabilis*.**

### **Introduction**

Landscape connectivity is fundamental to the dynamics of spatially structured animal populations (Fahrig and Merriam, 1985). It represents the degree to which the landscape facilitates or impedes the movement of individuals among resource patches and populations (Merriam, 1984; Taylor *et al.*, 1993). Recent studies using experimental model systems (EMS) (Crist *et al.*, 1992; With and Crist, 1995; Wiens *et al.*, 1997) have demonstrated complex, non-linear interactions between individual movement behavior and the structure of landscapes. For example, in their EMS analog to percolation models Wiens *et al.* (1997) observed that beetle movement within a particular cell (0.25m) in their experimental mosaic was contingent on the structure of the greater surrounding (micro)landscape (5 x 5m). In an earlier study involving the same organism, Crist *et al.*, (1992) suggest that, beyond vegetation structure, habitat affinity and thermoregulation may play important roles in governing individual movement behavior at some spatial scales.

From these and other empirical studies (e.g. Kareiva, 1987; Fahrig and Paloheimo, 1988) it is clear that we require an organism-centred view of landscape structure to adequately measure and understand landscape connectivity (Kareiva, 1987; Wiens *et al.*, 1993; Ims, 1995). Such an approach would recognize the potential influence of individual differences in behavior (Hassel and May, 1985), and encourage the contribution of species-specific behavioral ecology studies (Ives, 1995; Lima and Zolner, 1996). Indeed, to expose the causal mechanisms underlying structurally-mediated movement behaviors, empirical approaches should involve experiments designed in consideration of key behavioral or life history attributes (Wiens *et al.*, 1993; Price and Hunter, 1995). This includes, for example, the organism's dispersal capabilities - which helps define a relevant

experimental spatial scale (e.g. cabbage butterfly, Fahrig and Paloheimo, 1988), its habitat preferences (e.g. *Eleodes* beetles, Crist *et al.*, 1992), behaviors related to habitat quality (e.g. oviposition behavior, Ohgushi, 1995), territoriality (e.g. Capercaillie and root voles, Ims *et al.*, 1993), the internal states of individuals (e.g. starved versus unstarved caterpillar larvae, Cain *et al.*, 1983), and the environment - individual interactions that can influence the behavioral ecology of the organism (e.g. thermal ecology; Bach, 1984; Crist *et al.*, 1992; Solbreck, 1995).

Multi-scale experiments are required to reveal any relationships among scale-specific processes (Turner *et al.*, 1989; Johnson *et al.*, 1992; Wiens *et al.*, 1993). For example, can movement behaviors at fine spatial scales be used to predict distributions observed at broader scales? (e.g. Turchin, 1991). EMS have provided appropriate arenas for studying these relationships within certain small-scale systems (e.g. Kareiva, 1987; Crist *et al.*, 1992; Ims *et al.*, 1993; Wiens *et al.*, 1997); the key value of these studies has been in directing our attention to the more "sensitive" aspects of animal responses to landscape structure (Ims *et al.*, 1993). For example, in his habitat manipulation experiments (over ca. 18m), Kareiva (1987) demonstrated that habitat fragmentation promoted outbreaks of the prey species (aphids), because of reduced efficiency in the search behavior of their primary predators (ladybirds). Roland and Taylor (1997) later demonstrated similar relationships, at larger spatial scales, involving forest-tent caterpillars and four species of parasitic flies. They show that parasitism is significantly reduced or enhanced depending on the proportion of forested to unforested land. They also show that each parasitoid responds to fragmentation at a different spatial scale, corresponding to their relative body sizes.

To yield a more thorough understanding of landscape connectivity we require additional experiments at organism-defined spatial scales, that take account of scale-dependent processes and relationships at the individual level. Systems that allow

direct, real-scale analyses of landscape connectivity minimize the extent to which we depend on the (as yet) unproved process of extrapolating findings across scales (Turner *et al.*, 1989; Wiens *et al.*, 1993). By "real-scale" I mean scales at which key processes affecting regional population dynamics occur - such as dispersal.

*Calopteryx maculata* and *Calopteryx aequabilis* (Odonata: Calopterygidae) are relatively large damselflies, sympatric throughout my region, and locally abundant at streams where oviposition material (emergent aquatic vegetation) is abundant. Experiments have shown that the fine-scale (i.e. over several metres) distribution of adults along suitable streams is governed by the amount, dispersion, and quality of oviposition material (Alcock, 1987; Meek and Herman, 1990). The adults of both species are similar in their reproductive behaviors at the stream (Waage, 1975; Conrad and Herman, 1987; Meek and Herman, 1990). Females tend to be more vagile along the stream because of the territoriality of males at oviposition sites (Waage, 1972; Conrad and Herman, 1987; Meek and Herman, 1990). At small spatial scales (i.e. at reproductive sites) *C. aequabilis* shows a preference for sites with little shade, whereas *C. maculata* is shade-tolerant (Chapter 1). *C. aequabilis* is found more frequently at streams where forest is further than 50m away, and although *C. maculata* is often referred to as a forest species (Johnson, 1962; Waage, 1972; Forsythe and Montogmerie, 1987), it occurs at a similar proportion of sites across a range of forest proximities (Chapter 1). *C. maculata* does, however, appear to be more consistent than *C. aequabilis* in its use of forest as a resource (for foraging or roosting). Within pasture (i.e. non-forest) landscapes where forest patches are within ca. 500m of the stream habitat, *C. maculata* demonstrates continued use of forest resources by making daily transient flights through intervening pasture (non-resource) matrix (Taylor and Merriam, 1995). As a result, *C. maculata* individuals are distributed over land at greater distances from streams within pasture landscapes ( $284\pm 5\text{m}$ ) as compared to forest landscapes ( $189\pm 3\text{m}$ ) (Taylor and Merriam, 1995). I have observed a few *C.*



*aequabilis* individuals making similar directed flights, though not as consistently, nor over as much distance. When they occur within landscapes where forest is scarce (i.e. > ca. 500m from streams), both species appear to remain at the stream throughout the day, and evidently do not use forest as a resource.

While movement along streams is common (Henderson and Herman, 1984; Conrad and Herman, 1990), dispersal over land is likely to play an important role in these species' regional population dynamics, especially where, as in my study region, suitable streams and forest resources are patchily distributed and in relative proximity. Because residency time within a particular landscape element (and thus its connectivity) is contingent upon that element's suitability as a resource (Bach, 1984; Crist *et al.*, 1992; Bennett *et al.*, 1994), the behavioral variability observed within and among these damselfly species, with respect to forest as a preferred resource, provides a potentially useful detail around which to assess the connectivity of forest and pasture landscapes.

The purpose of this paper is to assess the relative abilities of *C. maculata* and *C. aequabilis* to move through forest and pasture landscapes, at a scale corresponding to dispersal distances typical to these species within my region. I define "pasture" to include any grassy, non-forested field.

In particular, my experiments are designed to test the following predictions:

1. The connectivity of pasture landscapes is higher than forest landscapes for both species, but the difference is more pronounced for *C. maculata*, which uses forest as a resource more consistently than *C. aequabilis*.
2. "Pasture" individuals (of both species) that do not use forest as a resource are apt to move more readily through forest than their forest-native counterparts, so I predict that the connectivity of forest landscapes will be higher for "pasture" individuals than "forest" individuals.
3. Because inter-sexual differences in movement behaviors at the stream are attributed to

territoriality in the males (Waage, 1972; Conrad and Herman, 1990; Meek and Herman, 1990), I predict no difference in the movement capabilities between the sexes (as is measured in my experiments) where territorial behavior does not occur.

## **Methods**

### *Study Region*

All experiments were performed on sunny, warm days ( $> 25^{\circ}\text{C}$ ) in the Annapolis Valley region of Nova Scotia, Canada ( $45^{\circ}05'\text{N}$ ;  $64^{\circ}30'\text{W}$ ) between June 25 and July 25 1996. My experiments make use of two types of structurally dissimilar landscapes: forest and pasture landscapes (Figure 2-1). Forest landscapes are common to the hills south of the valley, while pasture landscapes (defined here to include any grass fields) are dominant in the valley proper.

### *Field Experiments:*

#### *Verifying an appropriate experimental spatial scale*

I performed a preliminary experiment to determine whether reobservation rates of manipulated individuals would be limiting over 700m - a distance corresponding to typical dispersal distances in this region. This experiment is very similar in design to the main connectivity experiments. I describe it in detail below, reserving an explanation of the key differences in the designs for later. For this experiment I used only *C. maculata*, and assumed that the results would apply reasonably well to *C. aequabilis*.

On June 25, 1996 I captured and marked 50 individual *C. maculata* of each sex at a forested stream (Tupper Lake Brook, UTM: 374500m E 4987000m N). Only reproductive adults in good condition were used (i.e. wings were not damaged). Damselflies were caught using a standard insect flight net, and placed in a cooler at approximately  $10^{\circ}\text{C}$ . Alphanumeric markings were painted on the hind wings using thinned whiteout fluid (Forsyth and Montgomery, 1987). I displaced 10 of each sex at

distances of 350m and 700m from the stream at two different locales; one where the most direct route to their required stream habitat (there was only one stream in the vicinity) would take them through continuous forest, and the other where the most direct route was through patchily cut forest. These treatments were included to first verify whether the distance displaced affected my measures of connectivity, and secondly to test whether intermittent open areas along a displacement route would produce a detectable difference in connectivity as measured by reobservation rates. Ten "control" individuals of each sex were released at the stream, providing the expected proportion of the released individuals to be reobserved. Releases involved placing the cooled damselflies within a 1m<sup>3</sup> mesh cage, allowing them to acclimatize over 30 minutes, and opening the cage to allow them to fly away on their own accord. All groups were balanced according to the amount of time each individual endured captivity (all within two hours). Over the first three fair-weather days following the release (up to a maximum of six days), between 0900h and 1700h, I patrolled the stream for marked individuals. Reobservation effort included walking up and down a 350m section of the stream while agitating the streamside vegetation. Any marked individuals within sight of the stream counted as a reobservation. These tactics avoid biases in observation rates among sexes experienced by more passive observation (Henderson and Herman, 1984). Marked individuals are easily viewed with the naked eye, but 7x28 binoculars were used when required.

I analyze the results using logistic regression, with reobservation success as the binary response variable, and SEX, MATRIX and DISTANCE as the explanatory factors. The terms of interest in the resulting models will be the interactions between DISTANCE and all other factors. All statistical models presented were fit using the glm procedure in Splus (Chambers and Hastie, 1992). Residuals are deviance residuals (McCullagh and Nelder, 1989). I assessed the adequacy of fit of all models using residual diagnostics (McCullagh and Nelder, 1989).

I justify treating each damselfly as an independent observation in these models in two ways. First, I have seen no evidence to suggest that, when releasing the damselflies in groups away from the stream, they affect one another's movements. Similarly, when releasing them at the stream, where males are territorial, equal numbers are removed and replaced such that the density of damselflies before and after release would be the same. Second, weather conditions and release times are controlled for, such that each individual in each experiment receives roughly the same amount of manipulation and handling, all under similar environmental conditions.

### *Connectivity Experiments*

Figure 2-1 depicts a schematic representation of my connectivity experiments. They involve capturing, marking, and releasing groups of individual damselflies within and between landscapes of different structure - forest and pasture. Displaced individuals are released 700m away from a single stream (their required reproductive resource), and control individuals are released adjacent to the stream, providing the expected number to be reobserved. I equate the connectivity of the landscape with the proportion of displaced individuals observed to have reached the stream, as measured against the number of "control" individuals reobserved.

Of primary interest is whether forest and pasture landscapes facilitate movement to different degrees, i.e. is the connectivity of forest different from pasture, and in what direction? Reobservation rates according to the RELEASE landscapes (forest or pasture) will answer this question.

The reciprocal transplant portions of the experiments (Figure 2-1) allow us to assess the importance of individual qualities that may arise due to attributes of their SOURCE landscape. As described earlier, aspects of how these species use forest as a resource (for foraging or roosting) may be important in this regard. Is the connectivity of a forested

landscape affected by whether or not the animal made use of forest as a resource in its SOURCE landscape? This individual behavior aspect of connectivity is expressed in the SOURCE factor in my analyses.

Differences in connectivity according to the SEX of the individuals is also of interest. One full replicate experiment includes displacements of groups of both sexes within and among the pasture and forest landscapes (Figure 2-1). On some days and at some sites limited numbers of one sex allowed for only partial replicates (i.e. treatments on one sex) to be performed; i.e. it would take too long to capture enough of both sexes in one day. In these instances I attempted to complete the unfinished portion of the experiments on the next day, while allowing for continual reobservation by employing the help of an additional observer.

I was forced to use different landscapes for each species (logistically), therefore I analyze each species separately. As in the preliminary experiment, I analyze the results via logistic regression, with reobservation success as the binary response variable, and SEX, SOURCE, and RELEASE as the explanatory factors. Control and displaced individuals are distinguished in the models using the binary factor DISPLACE, so the terms of interest in the resulting models will be the interactions between DISPLACE and all other factors.

## **Results**

### *Verifying an appropriate experimental spatial scale*

A total of 17/50 (34%) of the males and 7/50 (14%) of the females were reobserved in the manipulative experiment. Based on the reobservations of control individuals (9/10 for males, and 4/10 for females), the expected proportion of each release group to be reobserved was 0.9 and 0.4 for males and females respectively. I reobserved an average of 35% of the expected number of individuals released at 350m, and 10% of those released at 700m (Figure 1-2). Thus distance had a significant effect (Table 2-1), but

there was no significant difference in the likelihood of reobserving individuals released in the continuous forest as compared to the patchy forest (effect of MATRIX, Table 1-1).

Thus reobservation rates were low, but not strictly limiting over 700m within forest landscapes. I predicted that they would be higher in pasture landscapes, and decided to proceed with the main connectivity experiments using 700m as the manipulative distance.

### *Connectivity Experiments*

Between June 25 and July 25, 1996, the total number of replicate experiments performed were 2.5 for male *C. maculata* (177 individuals), 1 for female *C. maculata* (44 individuals), 1.25 for male *C. aequabilis* (60 individuals), and 1.75 for female *C. aequabilis* (91 individuals). I always used an equal number of control versus displaced individuals. In two groups of male *C. maculata*, and one group of female *C. aequabilis*, these numbers were not equal due to mortalities within or near the release cages. The eight deaths (7 male *C. maculata*, and 1 female *C. aequabilis*) were caused by predation, likely when these individuals remained in the release cage, instead of flying away immediately after its opening. I found the marked wing remains of all of these individuals near the cage. It is less likely that predation occurred after the individuals flew outside of the cage.

Relative reobservation rates were similar in both RELEASE landscapes for *C. aequabilis* (Table 1-2), thus the connectivity of pasture landscapes appears to be similar to forest landscapes for this species. No effects were detected for the interactions between DISPLACE and the other factors SEX and SOURCE (Table 2-4).

Relative reobservation rates were significantly higher in pasture landscapes than in forest landscapes for *C. maculata* (Table 2-3), thus individuals moved more readily through pasture landscapes than through forest landscapes (effect of RELEASE; Table 2-5, Figure 2-3). Neither SEX NOR SOURCE landscape had a significant effect on relative

reobservation rates (Table 2-5), but pasture individuals were observed slightly more overall than forest individuals (not significant,  $p(\chi^2) = 0.116$ ) (Table 2-5).

## Discussion

I demonstrate that the connectivity of a landscape depends both on its structure, and on how that structure interacts with individual behavior to affect movement tendencies. I show that, although alike in many aspects of their ecology, *C. aequabilis* individuals move similarly through forest and pasture landscapes, while *C. maculata* move less readily through forest landscapes (effect of RELEASE,  $p(\chi^2) = 0.035$ ). Thus my prediction of higher connectivity of pasture landscapes was correct for *C. maculata*, but not for *C. aequabilis*. I did, however, predict that the magnitude of any difference in connectivity for *C. aequabilis* would be smaller than that observed for *C. maculata*, and given the observed magnitude of effect for *C. maculata* (parameter estimate = 0.80,  $t = 1.98$ ), the analyses may have required higher power (more replicate experiments) to be able to detect it.

My observations are consistent with the difference in how each species seems to perceive forest as a resource (Chapter 1). *C. maculata* individuals tend to use forest more consistently, and under more circumstances than *C. aequabilis*. My results thus agree with previous findings that residency times within a landscape element are generally longer when that element is perceived as a suitable resource by the animal (Bach, 1984; Crist *et al.*, 1992; Bennett *et al.*, 1994).

Although the movement behaviors of the sexes differ for both species at the stream (Waage, 1972; Conrad and Herman, 1987), I detected no differences in their relative abilities to move through forest or pasture matrix away from the stream. At the stream males are territorial at oviposition sites, and tend to be less vagile than females (Waage, 1972; Conrad and Herman, 1988). Away from the stream territoriality is not a factor, and I had no reason to expect differences in connectivity between the sexes.

I predicted an effect of SOURCE landscape on connectivity within my experiments. In particular, I predicted that "pasture" individuals (those that do not use forest as a resource) would move more readily through both landscapes than their forest-inhabiting counterparts. Again, I detected no such effects for *C. aequabilis*. For *C. maculata*, however, I did reobserve slightly more pasture individuals than forest individuals (effect of SOURCE,  $p(\chi^2) = 0.116$ ), again consistent with observations that residency times within a landscape element are generally longer when that element is perceived as a suitable resource by the individual (Bach, 1984; Crist *et al.*, 1992; Bennett *et al.*, 1994).

Considering the characteristics of my study region, my results suggest that inter-population dispersal for *C. maculata* is more likely to occur (over land) in the valley region than in the forested hills to the south. The valley supports a relatively dense network suitable streams and patchy forest, whereas streams in the southern hills are more sparsely distributed and the forest more continuous.

### **Summary**

The experimental design introduced here provided answers to fundamental questions concerning landscape connectivity, namely which of forest or pasture landscapes better permits movement over distances pertinent to the organisms' population dynamics? It enabled individual-based assessments of landscape connectivity, and exploited key variants of behavior in its design - the *intraspecific* in addition to *interspecific* behavioral variability in response to the spatial separation of two focal resources - streams (reproductive habitat) and forest (foraging habitat). I suggest that, if used in a number of other systems similarly chosen for key attributes (e.g. life-history traits), this experimental design could rapidly advance ecologists' understanding of landscape connectivity.



**Table 2-1.** Analysis of deviance table. Logistic regression of the likelihood of reobserving *C. maculata* individuals and experimentally controlled effects. Effects of interest are the interaction terms including the DISTANCE factor.

Effect	df	Deviance	p( $\chi^2$ )
Null	99	107.44	
DISTANCE	2	25.78	< 0.001
SEX	1	7.82	0.005
MATRIX	1	0.08	0.774
SEX X MATRIX	1	0.67	0.412
DISTANCE X SEX	2	1.94	0.380
DISTANCE X MATRIX	2	0.02	0.990
DISTANCE X SEX X MATRIX	2	2.25	0.324
Residual	88	68.87	

**Table 2-2.** Experimental reobservation rates for *C. aequabilis* individuals.

Treatment	Reobservation rate of control individuals	Reobservation rate of displaced individuals	Relative reobservation rate (column 2 ÷ column 1)
Released in forest*	43.3% (13/30)	6.9% (2/29)	15.9%
Released in pasture*	68.1% (32/47)	10.6% (5/47)	15.6%
Taken from forest†	48.1% (13/27)	11.5% (3/26)	23.9%
Taken from pasture†	64% (32/50)	8% (4/50)	12.5%

\* Effect of RELEASE landscape on reobservation rates, irrespective of SEX and SOURCE landscape.

† Effect of SOURCE landscape on reobservation rates, irrespective of SEX and RELEASE landscape.

**Table 2-3.** Experimental reobservation rates for *C. maculata* individuals.

Treatment	Reobservation rate of control individuals	Reobservation rate of displaced individuals	Relative reobservation rate (column 2 ÷ column 1)
Released in forest*	70.2% (40/57)	5.7% (3/53)	8.1%
Released in pasture*	61.1% (33/54)	17.5% (10/57)	28.6%
Taken from forest†	69.6% (48/69)	10.3% (7/68)	14.8%
Taken from pasture†	59.5% (25/42)	14.3% (6/42)	24.0%

\* Effect of RELEASE landscape on reobservation rates, irrespective of SEX and SOURCE landscape.

† Effect of SOURCE landscape on reobservation rates, irrespective of SEX and RELEASE landscape.

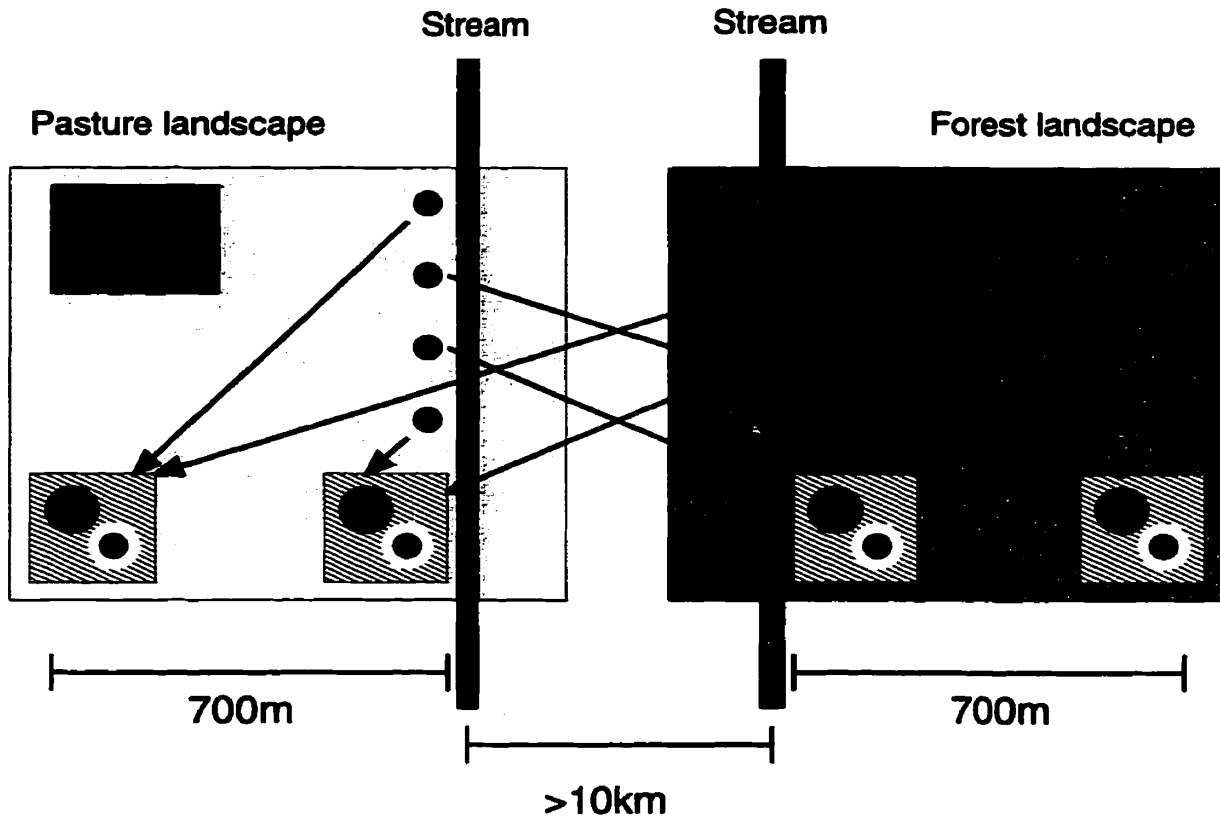
**Table 2-4.** Analysis of deviance table. Logistic regression of the likelihood of reobserving *C. aequabilis* individuals and experimentally controlled effects. Effects of interest are the interaction terms including the DISPLACE factor.

	df	Estimate	t value	Deviance	p ( $\chi^2$ )
Null	150	0.08	0.27		
DISPLACE	1	-2.75	-4.19	45.16	< 0.001
SEX	1	-0.09	-0.33	1.11	0.290
SOURCE	1	0.49	1.73	1.13	0.289
RELEASE	1	0.63	2.25	4.61	0.032
SOURCE X RELEASE	1	-0.35	-1.22	0.83	0.363
DISPLACE X SEX	1	-0.74	-1.19	1.45	0.229
DISPLACE X SOURCE	1	-0.77	-1.45	0.78	0.379
DISPLACE X RELEASE	1	-0.45	-0.86	0.25	0.617
DISPLACE X SOURCE X RELEASE	1	0.67	1.25	1.54	0.214
Residual	142			137.59	

**Table2-5.** Logistic regression of the likelihood of reobserving *C. maculata* individuals and experimentally controlled effects. Effects of interest are the interaction terms including the DISPLACE factor.

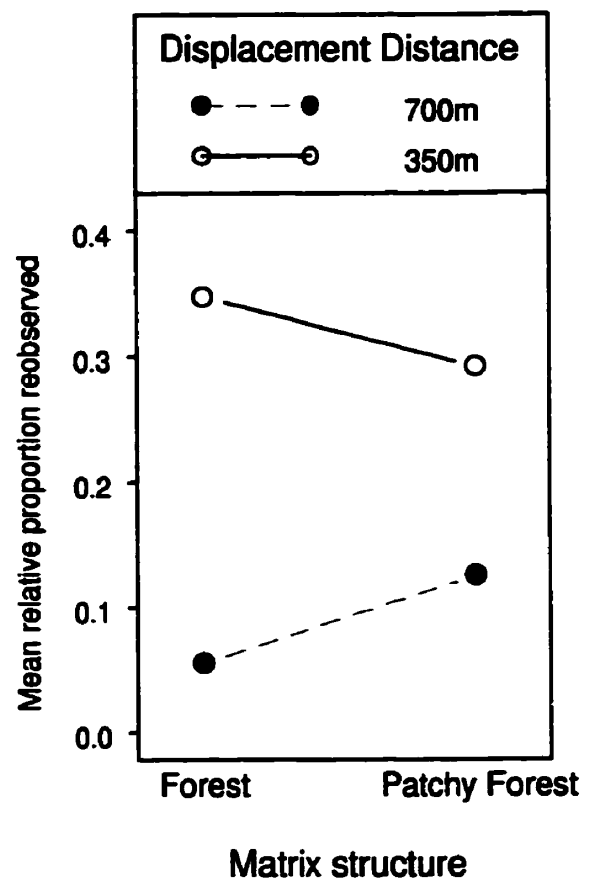
	df	Estimate	t value	Deviance	p ( $\chi^2$ )
Null	220	0.76	2.82	297.14	
DISPLACE	1	-2.49	-5.57	66.86	< 0.001
SEX	1	-0.24	-0.88	3.41	0.065
SOURCE	1	-0.24	-1.17	0.07	0.794
RELEASE	1	-0.16	-0.76	0.05	0.815
SOURCE X RELEASE	1	0.26	1.24	0.69	0.406
DISPLACE X SEX	1	-0.38	-0.92	0.94	0.332
DISPLACE X SOURCE	1	0.74	1.82	2.48	0.116
DISPLACE X RELEASE	1	0.80	1.98	4.47	0.035
DISPLACE X SOURCE X RELEASE	1	-0.57	-1.41	2.12	0.146
Residual	212			216.06	

**Figure 2-1.** Schematic diagram of one replicate of the connectivity experiments. Each circle represents a group of males and females (at least 6 of each, at most 10). Black circles represent individuals caught within pasture landscapes, and grey circles are forest individuals. Arrows indicate displacements within, and transfers between landscapes. Diagonally hatched boxes represent 1 m<sup>3</sup> cages.



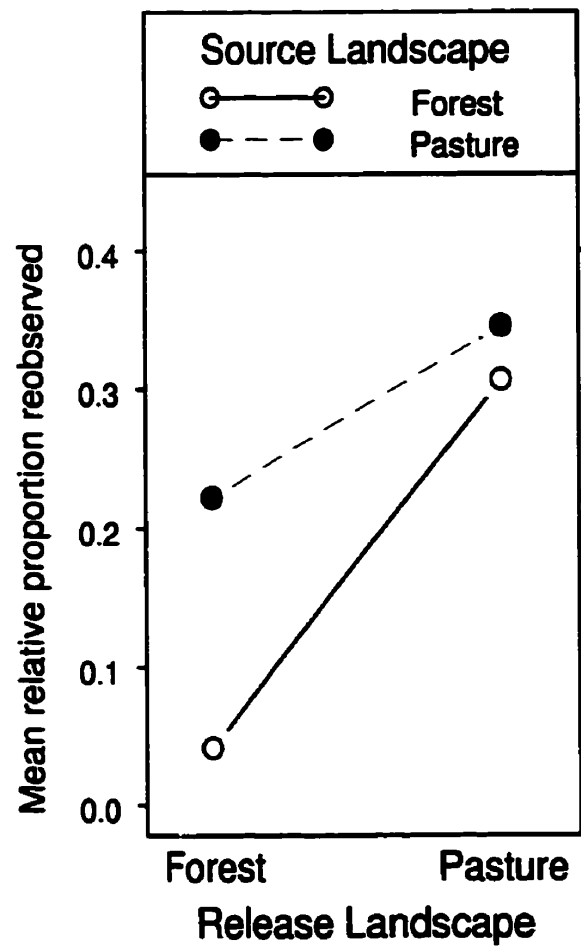
**Figure 2-2.** Interaction plot showing how the relative proportion of *C. maculata* individuals reobserved varies with DISPLACEMENT distance, but not with MATRIX type. The response variable is:

$(\# \text{ displaced individuals reobserved} / \# \text{ displaced}) \div$   
 $(\# \text{ control individuals reobserved} / \# \text{ controls released}).$



**Figure 2-3.** Interaction plot showing the effects of SOURCE landscape ( $p(\chi^2) = 0.116$ ) and RELEASE landscape ( $p(\chi^2) = 0.035$ ) on the mean relative proportion of displaced *C. maculata* individuals reobserved.





**Chapter 3. An assessment of fluctuating asymmetry and size in the wings of *Calopteryx maculata* and *Calopteryx aequabilis* in relation to landscape structure.**

**Introduction**

Fluctuating asymmetry (FA) refers to directionally random deviations from bilateral symmetry for a character pair of an organism (Leung and Forbes, 1997). FA arises when the stabilizing processes inherent to organism development (i.e. developmental homeostasis) are unable to buffer against disruptive factors during development (Palmer, 1994). Increased levels of FA - beyond those which are expected solely from the interplay of developmental "noise" and stabilizing processes - have been correlated with extreme conditions of environment (e.g. high levels of pollutants; Valentine and Soulé, 1973; Ames *et al.*, 1979), and restricted gene flow (e.g. inbreeding or genetic bottlenecks; Leary *et al.*, 1985; Wayne *et al.*, 1986). As such, its potential as a tool for monitoring stress levels in natural populations, and as an indicator of individual quality or fitness, has prompted much discussion and research (Leary and Allendorf, 1989; Leung and Forbes, 1997).

In this context, levels of FA have been examined among spatially structured animal populations (e.g. Patterson and Patton, 1990), and in particular, populations that have become subdivided by recent habitat fragmentation (e.g. Sarre, 1996; Wauters *et al.*, 1996). In both cases, extrinsic (i.e. environmental) and intrinsic (i.e. genetic) processes influence, to varying degrees, the phenotypes (e.g. behavior or morphology; West-Eberhard, 1992), and thus the fitness or quality of individuals (e.g. Wauters and Dhondt, 1989a).

These processes, and the rates at which they occur, are themselves mediated by landscape structure, and in particular landscape connectivity. For example, extrinsic pressures occur when structural changes to the landscape alter the territorial behaviors

(e.g. Ims *et al.*, 1993), foraging behaviors (e.g. Wauters *et al.*, 1992; Taylor and Merriam, 1995) or reproductive behaviors (e.g. Wauters *et al.*, 1990) of the animals. Intrinsic stresses (i.e. reduced heterozygosity) arise when population size is reduced to levels prone to inbreeding (e.g. Wayne *et al.*, 1986), and are exacerbated by decreased rates of dispersal among populations (e.g. Verboom and Apeldorn, 1990; Matthysen and Currie, 1996).

Landscape connectivity refers to the degree to which the landscape facilitates or impedes the movement of animals among habitat patches and populations (Merriam, 1984; Taylor *et al.* 1993). It is a function of the biology of the animal, and the behavioral response of the animal to the structure of the landscape (Merriam, 1991; Taylor *et al.*, 1993). Understanding how individuals respond to landscape structure *vis-a-vis* movement is an important step towards predicting how susceptible populations are to extrinsic and intrinsic pressures (Ims, 1995).

Data accumulated through several studies suggest to me that populations of the damselflies *Calopteryx aequabilis* and *Calopteryx maculata* (Odonata: Calopterygidae), are more isolated (i.e. less likely to encounter other populations or individuals from other populations) in forest landscapes than in moderately fragmented landscapes. First, in landscapes where forest (foraging habitat) is separated from their reproductive habitat (streams) by 200-500m, *C. maculata* individuals link the two resources by making directed flights through the intervening non-resource (pasture) matrix (Taylor and Merriam, 1995). I have observed a few *C. aequabilis* individuals making similar directed flights, though not as consistently, nor over as much distance. One consequence is that, on average, individuals in moderately fragmented pasture landscapes are distributed over a greater distance away from the stream than individuals inhabiting forested landscapes (Taylor and Merriam, 1995). Second, I conducted manipulative experiments to discover the relative abilities of individuals of both species to move through pasture and forest

landscapes, over a distance relevant to their regional population dynamics (Chapter 2). I found that pasture landscapes exhibit significantly higher connectivity than forest landscapes for *Calopteryx maculata*, while *C. aequabilis* moves similarly through both types of landscapes. Third, forested landscapes in my study region tend to support a lower density of suitable streams than do pasture landscapes.

Beyond these assessments concerning the relative isolation of populations (a possible intrinsic source of stress) I have no a priori reason to believe that damselfly populations in this region are experiencing any significant forms of stress; all sampled populations were healthy in numbers. Nonetheless, I was interested in examining the *patterns* of asymmetry (i.e. I do not restrict myself solely to the analysis of true FA) in the wings of *C. maculata* and *C. aequabilis* individuals, to determine if and how they correlate with those aspects of landscape structure that I have identified as being relevant to these species' natural histories. I compare wing asymmetries among *C. maculata* individuals captured within forest (low connectivity) and pasture (high connectivity) landscapes, and among *C. aequabilis* individuals captured at two pasture landscapes - one where forest is effectively absent (i.e. all individuals remain at the stream), and one where forest is near enough that a proportion of the damselflies may still access it.

I compare patterns of asymmetry among the sexes, and I suggest that the wings of males should be more symmetrical, on average, than those of females. Males of both species exhibit mating behaviors that may benefit directly from symmetrical wings. For example, the "courtship arc" involves the male hovering and bobbing up and down directly in front of a perched female (Waage, 1975; 1984; Conrad and Herman, 1987). It is possible that this behavior enables females to assess male quality - one aspect of which may be wing symmetry.

I also assess wing size (measures of length and width) as a function of landscape structure. Consistent with the adaptive foraging behaviors described earlier, Taylor and

Merriam (1995) found that the forewings of *C. maculata* individuals inhabiting pasture streams where extensive inter-resource movements are required were larger (after correcting for size) than those inhabiting forested streams. They proposed that there is micro-scale selection in moderately fragmented landscapes for individuals better suited to make those flights. I perform similar assessments to the extent that my data provide. In particular, I examine wing sizes in *C. maculata* individuals collected from high and low connectivity landscapes (i.e. pasture and forest respectively), and predict that individuals inhabiting the former sites will have larger wings on average than those inhabiting the forest streams. For *C. aequabilis* I assess wing sizes among two pasture sites. One of those sites is functionally similar to a forest site in that damselflies do not move far from the stream (the nearest forest is 800m away). The other site is within 500m of forest, and thus provides the opportunity for movement away from the stream. If indeed behavior begets morphological divergence in these damselflies, I predict that the wings of *C. aequabilis* individuals inhabiting the latter site will be larger, on average, than those of the individuals inhabiting the former site.

Taylor and Merriam (1995) also showed that wing size was more variable among pasture sites than among forest sites. Fragmented landscapes likely provide more opportunities for varied behavior (e.g. in foraging behavior, for example), so I predict that wing size will vary more within my high connectivity sites (pasture landscapes) than within my low connectivity sites (forest landscapes).

## **Methods**

A total of 131 male and 105 female *C. maculata*, and 41 male and 47 female *C. aequabilis* were captured using a standard insect flight net between June 29 (designated sampling week 1) and August 8 (week 5), 1996, at a number of streams within forest and pasture landscapes of the Annapolis Valley region of Nova Scotia, Canada. The

damselflies were placed in individual vials and stored in a freezer at approximately  $-10^{\circ}\text{C}$  until they were dissected in December 1996. The forewings, hindwings, and forelegs of each individual were clipped at their base, and fastened to acetate sheets using clear adhesive tape. They were then scanned at a resolution of 600dpi using a flatbed scanner with a background light source (i.e. a transparency adapter). I tested for any optical distortions by placing a stage micrometer at various locations on the scanner at orthogonal orientations a total of 20 times, and modeled pixel lengths using the freeware image analysis program ImageTools<sup>1</sup>. No distortions were detected.

Measurements were made on the scanned wing images using ImageTools. All measurements are analyzed and presented in pixel units. The landmarks used for measuring the left and right forewing lengths (FWL), forewing widths (FWW), hindwing lengths (HWL), and hindwing widths (HWW) are shown in Figure 3-1. These landmarks were chosen because they were the most readily identified on all the images. Femur lengths (FL) were measured from the joint with the trochanter to the joint with the tibia.

Numerous articles discuss the rigors of analyzing FA (e.g. Palmer and Strobeck, 1986; Yezerinac *et al.*, 1992; Cuthill *et al.*, 1993; Swaddle *et al.*, 1994; Merila and Bjorklund, 1995). I follow the suggestions of Palmer and Strobeck (1986), and heed the advice of Leung and Forbes (1997) regarding the potential importance of outliers and leptokurtic distributions of FA. In general there are three forms of asymmetry in nature: directional asymmetry (DA), which arises when one side of a character trait is consistently larger than the other, antisymmetry (AS), which is revealed through platykurtic distributions and has a number of possible origins (Palmer and Strobeck, 1992), and pure fluctuating asymmetry (FA), which exhibits a normal or leptokurtic distribution centred around zero (Leung and Forbes, 1997). Inferences regarding developmental stability in individuals can, strictly speaking, only be made among distributions of pure FA (Palmer, 1994). The

<sup>1</sup> A "Freeware" software program developed at University of Texas, Health Sciences, San Antonio

origins of, and confounds within each of the other forms of asymmetry are discussed in Palmer and Strobeck (1992).

Measurement errors (ME) are of particular concern in all analyses of FA (Palmer and Strobeck, 1986). FA itself can represent as little as 1-4% of character size (see examples in Palmer, 1994), while ME can contribute as much as 75% of that measured asymmetry for some traits (Palmer, 1994). To minimize ME, I measured each character twice, each time in a haphazard order, and each time blind to the source of each damselfly. In this way I could accurately account for the contribution of ME to observed FA. In the end, ME was generally less than 1% of forewing length measurements, and FA of *C. maculata* forewings was less than 4% of character size (Figure 3-2). Similar results were acquired for *C. aequabilis*.

Many of the damselflies used were recaptures from the manipulative experiments described previously, so the numbers captured during each week and at each site varied. My ultimate goal was to assess patterns of asymmetry and measures of wing size among individuals sampled from low and high connectivity LANDSCAPES, and among SITES within those LANDSCAPES. To provide datasets balanced by SITE and LANDSCAPE, I first eliminated individuals that were missing any of the measures, and subsequently drew random samples of equal numbers within each respective group. The resulting data sets and their structures were as follows (Note: in the end, of those individuals that were recaptures from the experiments, all but 6 of the were "controls" - i.e. not manipulated beyond marking):

1. Male *C. maculata*: 9 individuals per SITE, 2 measurements per individual, 3 sites {nested in} LANDSCAPE, 2 LANDSCAPES (low and high connectivity).
2. Female *C. maculata*: 14 individuals per SITE, 2 measurements per individual, 2 sites {nested in} each LANDSCAPE, 2 LANDSCAPES (low and high connectivity).
3. *C. aequabilis*: 13 individuals of each SEX per SITE, 2 measures per individual, 2 SITES.

The SEXES of *C. maculata* were analyzed separately to allow for larger sample datasets (and also, as shown in the results, because their asymmetry distributions are very

different).

The sites used for the *C. aequabilis* analyses were Dempsey's Corner (Dempsey) (UTM: 354300m E, 4990200m N) and Upper Dyke (UpDyke) (UTM: 383000m E, 4997000m N). The former site is situated approximately 500m south of forested hills, while the latter site is surrounded by intensive agricultural land; the nearest forest patch is over 800m away. At Dempsey, most individuals remain at the stream, but some access the nearby forest. Individuals inhabiting UpDyke remain at the stream and in the grasses adjacent to the stream.

I could not balance the data by week, and as such, my analyses may have been confounded. However, upon graphical inspection of individual size (average FL) versus sampling week using the subset data (Figure 3-3), I surmise that sampling week had little impact on my analyses of FA. Results regarding individual size variation and wing size variation among sites and landscapes should, however, be interpreted with caution.

Because methodology in analyses of FA is of particular concern (Palmer, 1994), I describe each analysis in detail below (henceforth, FA refers to signed (L-R) of the trait in question, unless otherwise noted). All analyses were performed using S-Plus (Chambers and Hastie, 1989).

#### *Patterns of wing asymmetry*

1. I first test for character-size dependence of signed (L-R) asymmetry with FWL by calculating their Pearson correlation coefficient. A significant result would require that FA be scaled before further analyses.
2. For *C. maculata*, the distributions of FWL and HWL of all individuals of each SEX were analyzed using 2-way, mixed model ANOVAS with left and ride SIDE as the fixed effect, and INDIVIDUAL as the random effect (Palmer and Strobeck, 1986). Variance due to ME was partitioned out by treating each repeated measurement as a pseudo-replicated



observation within an error term (this is essentially a repeated-measures ANOVA) (Chambers and Hastie, 1989). The terms of interest are as follows: a) DA is revealed by a significant effect of SIDE mean squares (MS) over the SIDE x INDIVIDUAL MS; b) Asymmetry due to variation among individuals is revealed by a significant effect of INDIVIDUAL MS over ME MS; and finally c) variation due to true FA *and* antisymmetry is revealed through a significant effect of the SIDE x INDIVIDUAL MS over the ME MS. If this term is not significant, further analyses are not warranted because measurement error is contributing too much variation overall.

3. To determine whether asymmetry (1c above) is in the form of true FA or antisymmetry, I provide measures of skew and kurtosis for each (L-R) distribution, and also examine histograms. If distributions are normal or leptokurtic (Leung and Forbes, 1997) about zero, then there is evidence for true FA.

4. I repeat steps 2 and 3 for each subset of data for *C. maculata*,

5. I perform steps 1-3 only on the subset data for *C. aequabilis*.

#### *Patterns of asymmetry and landscape structure*

All of the following analyses were performed on the subset data sets for each species respectively.

6. For each SEX separate ANOVAs were performed on the distributions of *signed* (L-R) FWL and (L-R) HWL of *C. maculata* individuals (similar to Levene's test) from each SITE {nested in} LANDSCAPE type (low or high connectivity). Variation due to ME was accounted for by including the factor INDIVIDUAL as an error term within the models. This serves to first fit a model of FA on each INDIVIDUAL represented as independent factors, then uses the residuals from that model as an additional term in the main ANOVA. A significant effect of LANDSCAPE indicates that the distributions of (L-R) are different in individuals among low and high connectivity landscapes. A significant effect of SITE {in}

LANDSCAPE indicates significant variation among signed L-R values of individuals inhabiting the various sites *within* each landscape type.

7. ANOVAs on the distributions of *signed* (L-R) FWL and HWL values for *C. aequabilis* were fit using the subset data including the factors SEX, SITE, and SEX x SITE.

As encouraged by Palmer and Strobeck (1992), I provide appropriate graphical depictions of the asymmetry data to aid in the interpretations. The results are somewhat voluminous, but provide a thorough representation of the data.

*Measures of wing size in relation to landscape structure*

8. FWLs and FWWs of *C. maculata* individuals were compared among LANDSCAPES and SITES within LANDSCAPES by fitting ANOVAs on the male and female subset data. (Note that my measurements are not actual wing lengths and widths, but I consider them related enough for the purpose of these analyses.) Because wing size depends on the general size of the individual, which in turn is a function of their naiad development habitat (Anholt, 1990), I first modeled the average femur length (FL) as a size covariate according to the main effects LANDSCAPE and SITE {in} LANDSCAPE. The SIZE RESIDUALS from this model are included in subsequent models (for both FWL and FWW) as an independent variable. Variation due to measurement error (ME) was also accounted for by including the factor INDIVIDUAL as an error term within the models. Analogous to fitting the size covariate (above), this serves to first fit a model of FA on each INDIVIDUAL represented as independent factors, then uses the residuals from that model as an additional term in the main ANOVA. The difference here is that I am not interested in the effects of ME, and so I don't explicitly represent the full ME model within my ANOVA tables - the effects are summarized in one level of the ANOVA. In the main models, significant effects of LANDSCAPE on FWL or FWW would indicate that wing lengths or wing widths differ

among the two types of landscape, even after accounting for individual size.

9. I fit an ANOVA on the FWL and FWW of *C. aequabilis* individuals, using the subset data, testing for the effects of SEX or SITE. As in (8), I first fit FL as a size covariate, and include the residuals as an independent term in the main model.

All figures depicting measurement values of some sort used values derived from the first set of repeated measurements unless otherwise noted. The error distributions of the data were normal, and required no transformations.

## Results

My assessment of character-size dependence of FA revealed no significant correlation between FWL and average |L-R| forewing lengths for male *C. maculata* (Pearson correlation coefficient,  $r = -0.10$ ,  $df = 111$ ,  $p > 0.1$ ) nor for females ( $r = -0.15$ ,  $df = 94$ ,  $p > 0.1$ ) (Figure 3-4). Similarly, no relationship was evident in *C. aequabilis* (males:  $r = 0.04$ ,  $df = 38$ ,  $p = 0.8$ ; females:  $r = -0.06$ ,  $df = 42$ ,  $p = 0.7$ ). Thus I did not transform any data for the subsequent analyses.

### *Patterns of wing asymmetry*

I found significant amounts of DA (effect of SIDE), and evidence for either antisymmetry or true FA (effect of SIDE x INDIVIDUAL) in FWLs across all male *C. maculata* individuals (Table 3-1). There was also considerable variation among individuals (effect of INDIVIDUAL). Inspection of the histogram of FA (Figure 3-5) shows the curious result that right wings are consistently larger than left wings in most males. In females I found considerable INDIVIDUAL variation, and evidence for antisymmetry or true FA (Table 3-2), but no evidence for DA. The distribution of (L-R) FWL for males was not particularly skewed ( $G_1 = -0.06$ ), but did show evidence of platykurtosis ( $G_2 = -0.54$ ) (Figure 3-6). Inferences regarding true FA, therefore, cannot be made in male *C. maculata*. For

females, the distribution was skewed slightly right ( $G_1 = 0.29$ ), and showed signs of leptokurtosis ( $G_2 = 0.18$ ) (Figure 3-6). Because skew of this sort (Figure 3-6) is a possible outcome of the interaction of DA and antisymmetry (Palmer and Strobeck, 1992), I cannot interpret asymmetry distributions in female *C. maculata* forewings as exhibiting true FA.

The distribution of (L-R) HWL in male *C. maculata* revealed different results again. Male hindwings were not directionally asymmetrical (Table 3-3) (Figure 3-7), and their (L-R) distribution was less platykurtic than that for FWL ( $G_2 = -0.31$ ) (Figure 3-8). Female distributions of (L-R) HWL were again skewed right ( $G_1 = 0.32$ ), but not as leptokurtic as (L-R) FWL ( $G_2 = 0.08$ ) (Figure 3-8). Both distributions are not indicative of true FA.

The male and female *C. maculata* subset datasets showed identical overall patterns in both (L-R) FWL and (L-R) HWL distributions to those of the full datasets. I do not present these results.

I do not assess general FA using the full data sets for *C. aequabilis*, but I provide their histograms (Figure 3-9). Again, distributions depart from ideal FA, so the data are interpreted in terms of general patterns of asymmetry.

*C. aequabilis* subset males and females exhibited considerable amounts of variation among individuals in both the distributions of (L-R) FWL and (L-R) HWL (effect of INDIVIDUAL; Tables 3-5 through 3-8). Note that contrary to what was observed in *C. maculata* individuals, it is the females of *C. aequabilis* that show a trend towards DA in (L-R) FWL (effect of SIDE; Table 3-6). The distribution of (L-R) FWL in males was only slightly skewed left, and showed no evidence of platykurtosis or leptokurtosis ( $G_1 = -0.19$ ;  $G_2 < 0.01$ ). Female distributions of (L-R) FWL were skewed right and leptokurtic ( $G_1 = 1.04$ ;  $G_2 = 1.27$ ).

*FA and landscape structure*

I found no significant differences in the distributions of either (L-R) FWL and (L-R) HWL among *C. maculata* individuals of either sex native to high connectivity (pasture) and low connectivity (forest) landscapes (Tables 3-9 through 3-12). Nor were there any effects of SITE on asymmetry patterns in *C. maculata*.

*C. aequabilis* individuals from UpDyke exhibited higher levels of |L-R| FWL than Dempsey individuals (Figure 3-10). This effect was consistent among the sexes, but most pronounced for females.

#### *Measures of wing size in relation to landscape structure*

The size of male *C. maculata* individuals varied according to site (Table 3-15), and after controlling for the effects of SIZE, I found a marginal effect of SITE {in} LANDSCAPE on the FWL (Table 3-16). Individuals inhabiting sites within the high connectivity landscapes (pasture) exhibited more variation in FWL than their forest-dwelling counterparts (Figure 3-11). Female *C. maculata* size depended on LANDSCAPE type (Table 3-18), and after controlling for SIZE effects, I found a marginal effect of LANDSCAPE on FWL (Table 3-19; Figure 3-12).

The size of *C. aequabilis* individuals did not differ among SITES, nor among the SEXES (Table 3-21). After controlling for SIZE, however, there were highly significant effects of SEX and SITE on FWLs of *C. aequabilis* individuals (Table 3-22), and an effect of SEX on FWW (Table 3-23; Figure 3-13). Females had significantly larger wings than males, and individuals of both sexes had longer wings at Dempsey than at UpDyke (Figure 3-14).

## Discussion

### *Patterns of wing asymmetry and their relation to landscape structure*

Through previous work I determined that the propensity of *C. maculata* individuals to move over land is higher within pasture landscapes - especially where forest and stream resources are moderately separated in space - than in forest landscapes. In my study region, forested streams tend also to be more spatially isolated than pasture streams. I thus suggested that damselflies inhabiting forested landscapes are, relatively speaking, more "isolated" than those inhabiting pasture landscapes. I examined wing asymmetry in groups of damselflies collected from sites within these landscapes, to see if patterns were in some way consistent with my designations of connectivity.

I found no detectable differences in the patterns of asymmetry of the fore and hindwings of *C. maculata* individuals collected from sites within high connectivity and low connectivity landscapes. Asymmetry levels throughout *C. maculata* and *C. aequabilis* populations sampled were consistently less than 4% of character length (Figure 3-2). Harvey and Walsh (1993) found similarly small levels of asymmetry in the forewings of *Coenagrion* damselflies, and their estimates were probably inflated compared to mine due to measurement error. I did find a significant difference in the distributions of (L-R) FWL for *C. aequabilis* individuals inhabiting different pasture sites (Table 3-13). UpDyke individuals exhibited larger magnitudes of |L-R| FWL than Dempsey individuals. UpDyke is a site where forest resources are absent, and damselflies remain at the stream throughout the day. At Dempsey, some individuals may continue to use forest that is within 500m. I will not speculate as to whether or not this is related to the observed differences.

That I found a strong trend of directional asymmetry within forewings of all male *C. maculata* is somewhat surprising. Right wings were consistently longer than left wings (Figure 3-5). I had proposed that males should benefit from more symmetrical wings

because of their function not only in locomotion, but also in mating behaviors (Conrad and Herman, 1987; Meek and Herman, 1990). Harvey and Walsh (1993) found leptokurtic distributions of FA in the wings of *Coenagrion* damselflies, a result consistent with the proposal that symmetrical wings are favoured, and that individuals exhibiting extreme asymmetry should experienced increased mortality during maturation periods (Leung and Forbes, 1997). Directional asymmetry is relatively rare in nature (Palmer and Strobeck, 1986), and why it is prevalent in these *C. maculata*, and not in *C. aequabilis*, is unknown. Curiously, I found that hind wings in male *C. maculata* were not the same as forewings in their patterns of asymmetry (Table 3-3). Within-individual inconsistencies of true FA (which, strictly speaking, I do not see) have been observed elsewhere (e.g. Manning and Chamberlain, 1994), and raise the question of which traits are reliable indicators (if any) of stress? Sexually selected traits have been proposed as better indicators of fitness (e.g. Møller, 1990), but recently, Leung and Forbes (1997) demonstrated theoretically that FA within those traits need not relate to stress or fitness any better than FA within other traits. More importantly, they demonstrate that FA of some characters need not relate to stress or quality at all.

#### *Wing size in relation to landscape structure*

Taylor and Merriam (1995) showed elsewhere that the forewings of *C. maculata* individuals inhabiting pasture streams where extensive inter-resource movements are required were larger (after correcting for size) than those inhabiting forested streams. I also see evidence for this trend in my data. First, after correcting for the effects of SIZE, the FWL of female *C. maculata* individuals inhabiting high connectivity landscapes (pasture streams) were longer than those inhabiting low connectivity landscapes (forest streams) (Table 3-19; effect of LANDSCAPE,  $p(F) = 0.076$ ). Second, *C. aequabilis* forewings were significantly longer (after accounting for SIZE) in individuals inhabiting Dempsey

than those at UpDyke. The former site provides opportunity for movement among resources away from the stream, whereas individuals at the latter site remain at the stream. Overall trends in the data also show consistencies in this regard. Figure 3-11 shows wing lengths for each sex plotted by SITE, and the SITES are arranged in increasing degrees of forest fragmentation, to a maximum degree at the site Dempsey - the same site described above. "Newc" is similar to Dempsey in that there are forest patches within several hundred metres. Both of these sites (both within the high connectivity landscapes) support individuals with longer forewings on average than those at other sites (Table 3-16 for males, effect of SITE  $\{in\}$  LANDSCAPE,  $p(F) = 0.059$ ; Table 3-19 for females, effect of LANDSCAPE,  $p(F) = 0.076$ ). "Black" is a less fragmented site (i.e. forest is within 100m) within the high connectivity landscape type, and individuals there had forewing lengths similar to the low connectivity sites. Because there are likely more opportunities for varied behavior within fragmented forest landscapes (Taylor and Merriam, 1995), I had predicted that wing size would vary more among sites within high connectivity landscapes (pasture) than among sites within low connectivity landscapes (forest). These results support this prediction.

Unlike the findings of Taylor and Merriam (1995), forewing widths in my region were not significantly related to landscape structure. The different ways in which wings were measured in each study may explain the differences: my measurements of wing widths depended heavily on patterns of wing venation moreso than my measures of wing length (this made them particularly suitable for measuring FA) (see Figure 3-1). As such, they were less likely to be accurate representations of true wing width than those in Taylor and Merriam (1995). My wing length measurements, however, were made along a vein that runs directly lengthwise on all wings (Figure 3-1), and were thus more accurate relative measures of true wing length.



## **Summary**

Ideal FA was not evident in the distributions of (L-R) forewing lengths or hindwing lengths of *C. maculata* or *C. aequabilis*. For unknown reasons, right forewings were consistently longer than left forewings in male *C. maculata* individuals. Hindwings did not follow this trend. The patterns of asymmetry in fore and hindwing lengths were consistent among LANDSCAPES and SITES, for both sexes of both species.

Forewing lengths of *C. maculata* were, on average, longer within high connectivity landscapes (pasture) than in low connectivity landscapes (forest). They were also more variable within high connectivity (pasture) landscapes than in low connectivity (continuous forest) landscapes. The forewings of *C. aequabilis* individuals inhabiting a stream within an extremely fragmented landscape (i.e. no forest available) had shorter wings than individuals inhabiting a moderately fragmented landscape.

Wing morphologies are thus consistent with the behavioral differences observed among populations of the damselflies *C. maculata* and *C. aequabilis*, and those behavioral differences arise due to structural attributes of their host landscapes.

**Table 3-1: Mixed model analysis of variance table. The response variable is forewing FA (pixels) of all male *Calopteryx maculata* individuals.**

	Df	MS	F	p(F)
Null				
SIDE	1	422.47	37.96	< 0.01
INDIVIDUAL	122	247.78	355.49	< 0.01
SIDE X INDIVIDUAL	122	11.13	15.97	< 0.01
MEASUREMENT ERROR	246	0.697		

**Table 3-2: Mixed model analysis of variance table. The response variable is forewing FA (pixels) of all female *Calopteryx maculata* individuals.**

	Df	MS	F	p(F)
Null				
SIDE	1	11.82	1.12	ns
INDIVIDUAL	99	425.70	686.61	< 0.01
SIDE X INDIVIDUAL	99	10.58	17.06	< 0.01
MEASUREMENT ERROR	200	0.62		

**Table 3-3: Mixed model analysis of variance table. The response variable is hindwing FA (pixels) of all male *Calopteryx maculata* individuals.**

	Df	MS	F	p(F)
Null				
SIDE	1	82.34	3.62	0.05 < p < 0.10
INDIVIDUAL	114	201.63	62.42	< 0.01
SIDE X INDIVIDUAL	114	22.75	7.04	< 0.01
MEASUREMENT ERROR	230	3.23		

**Table 3-4: Mixed model analysis of variance table. The response variable is hindwing FA (pixels) of all female *Calopteryx maculata* individuals.**

	Df	MS	F	p(F)
Null				
SIDE	1	13.98	1.30	ns
INDIVIDUAL	93	295.10	567.5	< 0.01
SIDE X INDIVIDUAL	93	10.72	20.62	< 0.01
MEASUREMENT ERROR	188	0.52		

**Table 3-5: Mixed model analysis of variance table. The response variable is forewing FA (pixels) of subset male *Calopteryx aequabilis* individuals.**

	Df	MS	F	p(F)
Null				
SIDE	1	2.50	0.21	ns
INDIVIDUAL	25	589.60	1551.58	< 0.01
SIDE X INDIVIDUAL	25	11.78	31.00	< 0.01
MEASUREMENT ERROR	52	0.38		

**Table 3-6: Mixed model analysis of variance table. The response variable is forewing FA (pixels) of subset female *Calopteryx aequabilis* individuals.**

	Df	MS	F	p(F)
Null				
SIDE	1	56.77	3.26	0.05 < p < 0.10
INDIVIDUAL	25	420.36	1273.82	< 0.01
SIDE X INDIVIDUAL	25	17.41	52.76	< 0.01
MEASUREMENT ERROR	52	0.33		

**Table 3-7: Mixed model analysis of variance table. The response variable is hindwing FA (pixels) of subset male *Calopteryx aequabilis* individuals.**

	Df	MS	F	p(F)
Null				
SIDE	1	5.77	0.62	ns
INDIVIDUAL	25	410.81	893.06	< 0.01
SIDE X INDIVIDUAL	25	9.27	20.15	< 0.01
MEASUREMENT ERROR	52	0.46		

**Table 3-8: Mixed model analysis of variance table. The response variable is hindwing FA (pixels) of subset female *Calopteryx aequabilis* individuals.**

	Df	MS	F	p(F)
Null				
SIDE	1	12.04	1.05	ns
INDIVIDUAL	25	343.65	536.95	< 0.01
SIDE X INDIVIDUAL	25	11.45	17.89	< 0.01
MEASUREMENT ERROR	52	0.64		

**Table 3-9:** Analysis of variance table. The response variable is forewing FA (pixels) of subset male *Calopteryx maculata* individuals from high and low connectivity landscapes.

	Df	MS	F	p(F)
Null				
MEASUREMENT ERROR	54	1.51	0.08	ns
LANDSCAPE	1	38.37	1.99	ns
SITE (IN) LANDSCAPE	4	22.32	1.16	ns
Residual	48	19.31		

**Table 3-10:** Analysis of variance table. The response variable is forewing FA (pixels) of subset female *Calopteryx maculata* individuals from high and low connectivity landscapes.

	Df	MS	F	p(F)
Null				
MEASUREMENT ERROR	56	0.76	0.04	ns
LANDSCAPE	1	5.73	0.30	ns
SITE (IN) LANDSCAPE	2	5.09	0.26	ns
Residual	52	19.23		

**Table 3-11:** Analysis of variance table. The response variable is hindwing FA (pixels) of subset male *Calopteryx maculata* individuals from high and low connectivity landscapes.

	Df	MS	F	p(F)
Null				
MEASUREMENT ERROR	54	1.15	0.02	ns
LANDSCAPE	1	2.22	0.04	ns
SITE (IN) LANDSCAPE	4	129.65	2.24	ns
Residual	48	57.79		

**Table 3-12:** Analysis of variance table. The response variable is hindwing FA (pixels) of subset female *Calopteryx maculata* individuals from high and low connectivity landscapes.

	Df	MS	F	p(F)
Null				
MEASUREMENT ERROR	56	1.18	0.05	ns
LANDSCAPE	1	13.20	0.60	ns
SITE (IN) LANDSCAPE	2	8.54	0.39	ns
Residual	52	21.89		

**Table 3-13:** Analysis of variance table. The response variable is forewing FA (pixels) of subset *Calopteryx aequabilis* individuals from one moderately fragmented site and one highly fragmented site.

	Df	MS	F	p(F)
<b>Null</b>				
MEAS. ERROR	52	0.55	0.06	ns
SEX	1	24.68	2.61	0.11
SITE	1	35.85	3.79	0.052
SEX X SITE	1	2.00	0.21	0.65
Residual	48	9.46		

**Table 3-14:** Analysis of variance table. The response variable is hindwing FA (pixels) of subset *Calopteryx aequabilis* individuals from one moderately fragmented site and one highly fragmented site.

	Df	MS	F	p(F)
<b>Null</b>				
MEAS. ERROR	52	0.78	0.09	ns
SEX	1	2.63	0.28	0.59
SITE	1	0.32	0.03	0.85
SEX X SITE	1	0.00	0.00	0.99
Residual	48			

**Table 3-15:** Analysis of variance table. The response variable is average femur length (pixels) of subset male *Calopteryx maculata* individuals from high and low connectivity landscapes. The model errors are from a normal distribution. Residuals from this model are used as an independent variable (size residuals) in the FWL and FWW models for males (Table 3-16, Table 3-17).

	Df	MS	F	p(F)
Null				
LANDSCAPE	1	6.55	0.28	0.642
SITE {IN} LANDSCAPE	4	111.28	3.69	0.008
Residual	102	30.13		

**Table 3-16:** Analysis of variance table. The response variable is forewing length (pixels) of subset male *Calopteryx maculata* individuals from high and low connectivity landscapes. MEAS. ERROR is fit as an error term within the model.

	Df	MS	F	p(F)
Null				
MEAS. ERROR	54			ns
SIZE RESIDUALS	1	663.06	6.10	0.018
LANDSCAPE	1	93.46	0.86	0.359
SITE {IN} LANDSCAPE	4	268.97	2.47	0.059
LANDSCAPE X SIZE RESIDUALS	1	58.99	0.79	0.379
(SITE {IN} LANDSCAPE) X SIZE	4	69.46	0.64	0.638
RESIDUALS				
Residual	42	108.75		

**Table 3-17:** Analysis of variance table. The response variable is forewing width (pixels) of subset male *Calopteryx maculata* individuals from high and low connectivity landscapes. MEAS. ERROR is fit as an error term within the model.

	Df	MS	F	p(F)
Null				
MEAS. ERROR	54			ns
SIZE RESIDUALS	1	691.78	8.09	0.007
LANDSCAPE	1	8.49	0.10	0.754
SITE {IN} LANDSCAPE	4	91.57	1.07	0.383
LANDSCAPE X SIZE RESIDUALS	1	5.02	0.06	0.810
(SITE {IN} LANDSCAPE) X SIZE	4	53.01	0.62	0.651
RESIDUALS				
Residual	42	85.54		

**Table 3-18:** Analysis of variance table. The response variable is average femur length (pixels) of subset female *Calopteryx maculata* individuals from high and low connectivity landscapes. The model errors are from a normal distribution. Residuals from this model are used as an independent variable (size residuals) in the female FWL and FWW models (Table 3-19, Table 3-20).

	Df	MS	F	p(F)
<b>Null</b>				
LANDSCAPE	1	160.70	4.92	0.029
SITE (IN) LANDSCAPE	2	66.99	2.05	0.134
<b>Residual</b>	<b>108</b>	<b>32.67</b>		

**Table 3-19:** Analysis of variance table. The response variable is forewing length (pixels) of subset female *Calopteryx maculata* individuals from high and low connectivity landscapes. MEAS. ERROR is fit as an error term within the model.

	Df	MS	F	p(F)
<b>Null</b>				
MEAS. ERROR	56			ns
SIZE RESIDUALS	1	392.11	1.78	0.188
LANDSCAPE	1	725.96	3.30	0.076
SITE (IN) LANDSCAPE	2	215.17	0.98	0.384
LANDSCAPE X SIZE RESIDUALS	1	1223.06	5.55	0.023
(SITE (IN) LANDSCAPE) X SIZE	2	300.95	1.37	0.265
<b>RESIDUALS</b>				
<b>Residual</b>	<b>48</b>	<b>220.32</b>		

**Table 3-20:** Analysis of variance table. The response variable is forewing width (pixels) of subset female *Calopteryx maculata* individuals from high and low connectivity landscapes. MEAS. ERROR is fit as an error term within the model.

	Df	MS	F	p(F)
<b>Null</b>				
MEAS. ERROR	56			ns
SIZE RESIDUALS	1	46.32	0.37	0.544
LANDSCAPE	1	29.67	0.24	0.627
SITE (IN) LANDSCAPE	2	150.73	1.22	0.305
LANDSCAPE X SIZE RESIDUALS	1	7.04	0.06	0.813
(SITE (IN) LANDSCAPE) X SIZE	2	50.22	0.41	0.669
<b>RESIDUALS</b>				
<b>Residual</b>	<b>48</b>	<b>123.86</b>		

**Table 3-21:** Analysis of variance table. The response variable is average femur length (pixels) of subset *Calopteryx aequabilis* individuals from one moderately fragmented site and one highly fragmented site. The model errors are from a normal distribution. Residuals from this model are used as an independent variable (size residuals) in the FWL and FWW models (Table 3-22, Table 3-23).

	Df	MS	F	p(F)
<b>Null</b>				
SEX	1	145.61	1.40	0.240
SITE	1	64.06	0.61	0.435
SEX X SITE	1	238.22	2.28	0.134
<b>Residual</b>	<b>100</b>	<b>104.34</b>		



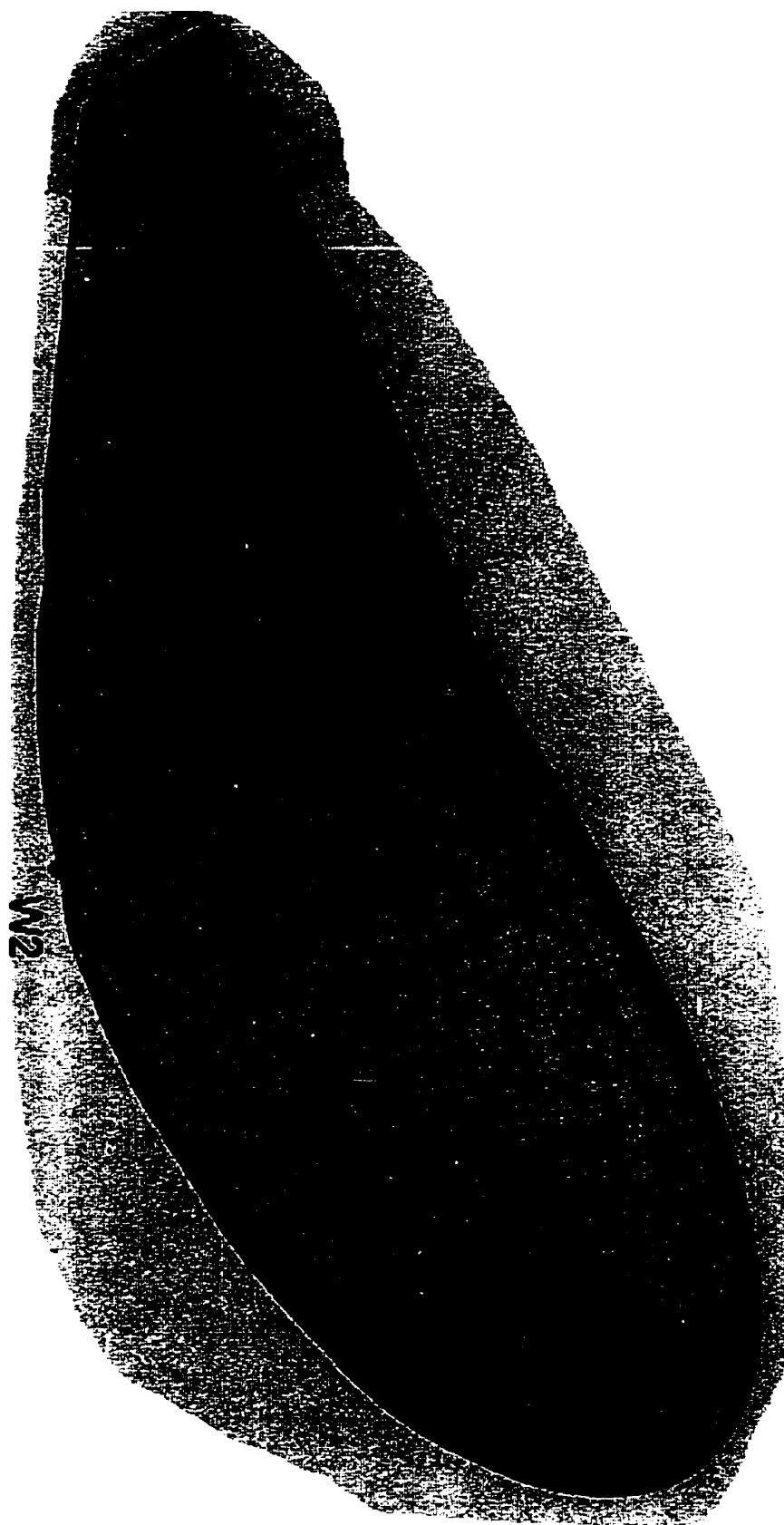
**Table 3-22:** Analysis of variance table. The response variable is forewing length (pixels) of subset *Calopteryx aequabilis* individuals from one moderately fragmented site and one highly fragmented site. MEAS. ERROR is fit as an error term within the model.

	Df	MS	F	p(F)
Null				
MEAS. ERROR	52			ns
SIZE RESIDUALS	1	81.26	0.39	0.534
SEX	1	7113.19	34.31	< 0.001
SITE	1	2738.81	13.21	< 0.001
SIZE RESIDUALS X SEX	1	117.32	0.57	0.456
SIZE RESIDUALS X SITE	1	372.03	1.79	0.187
SEX X SITE		7.35	0.04	0.852
SIZE RESIDUALS X SEX X SITE	1	186.36	0.90	0.348
Residual	44	207.30		

**Table 3-23:** Analysis of variance table. The response variable is forewing width (pixels) of subset *Calopteryx aequabilis* individuals from one moderately fragmented site and one highly fragmented site. MEAS. ERROR is fit as an error term within the model.

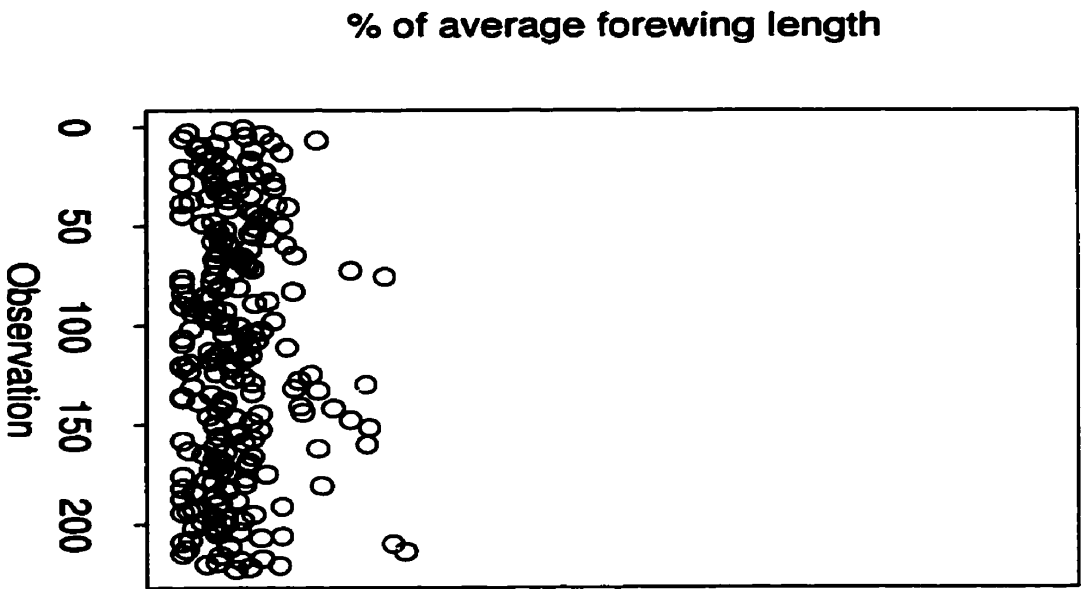
	Df	MS	F	p(F)
Null				
MEAS. ERROR	52			ns
SIZE RESIDUALS	1	17.75	0.26	0.616
SEX	1	1165.87	16.78	< 0.001
SITE	1	15.25	0.22	0.642
SIZE RESIDUALS X SEX	1	0.93	0.01	0.908
SIZE RESIDUALS X SITE	1	210.22	3.03	0.089
SEX X SITE		5.50	0.08	0.780
SIZE RESIDUALS X SEX X SITE	1	32.23	0.46	0.500
Residual	44	69.47		

**Figure 3-1.** An example scanned image of a right forewing of a *C. maculata* female. Shown are the landmarks used to measure wing lengths (L1 to L2) and wing widths (L2 to W1).

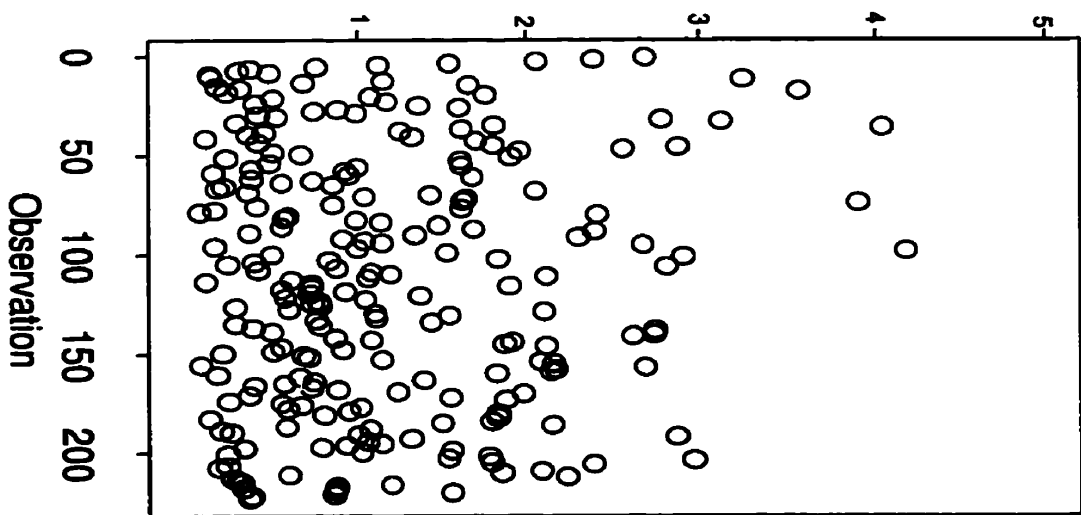


**Figure 3-2.** Scatter plots of (A) the measurement error in forewing lengths and (B) unsigned asymmetry as a percentage of total forewing length.

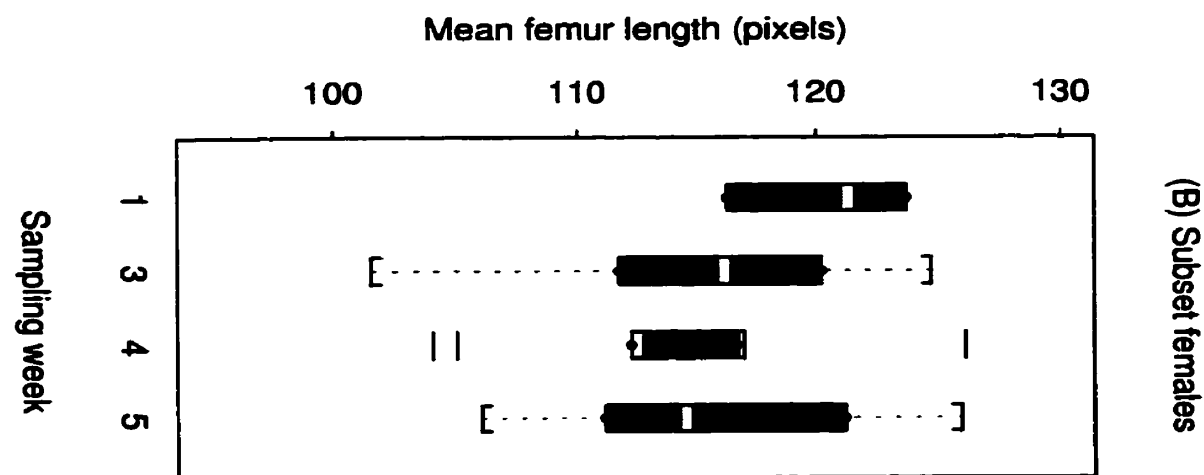
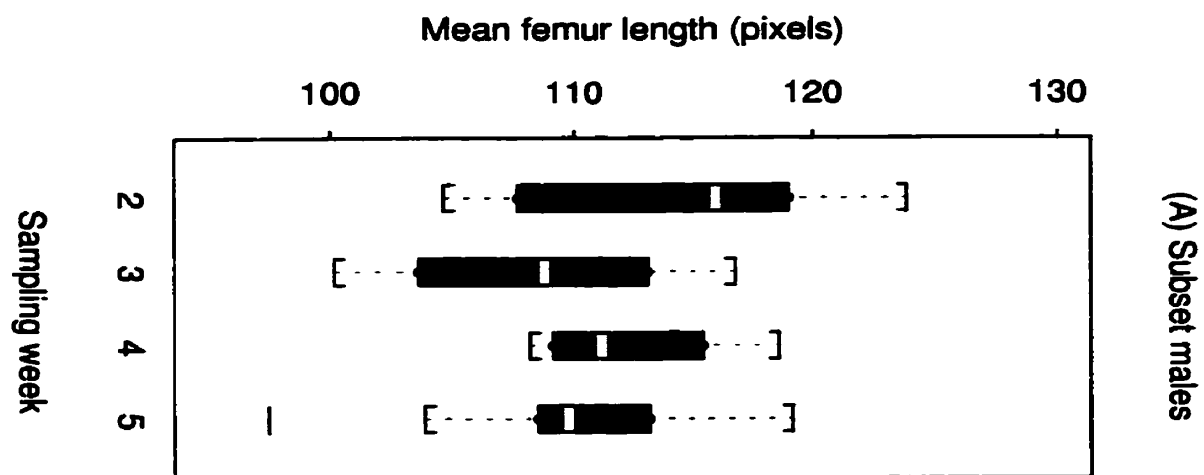
(A) Measurement error



(B) |L-R| forewing length



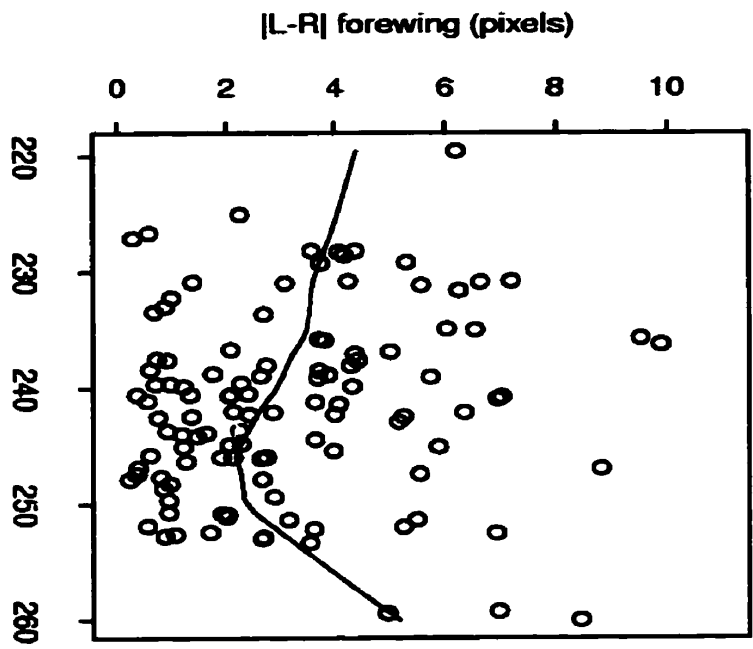
**Figure 3-3.** Boxplots showing median (white bar), interquartile range (box), range (whiskers), and outliers (bars) of mean femur lengths of (A) subset male and (B) subset females by sampling week (week 1 = June 29, 1996).



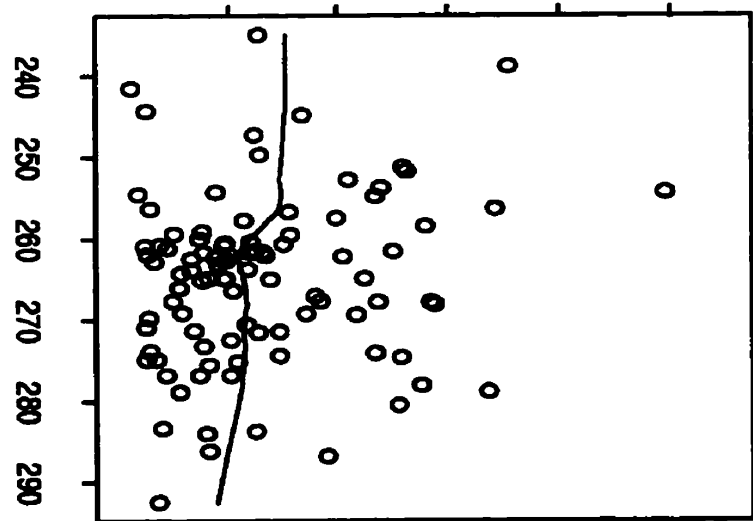
**Figure 3-4.** Scatter plots of unsigned forewing asymmetry versus average forewing length in (A) male *C. maculata* and (B) female *C. maculata*. Lines are lowess smoothing curves.



(A) All males



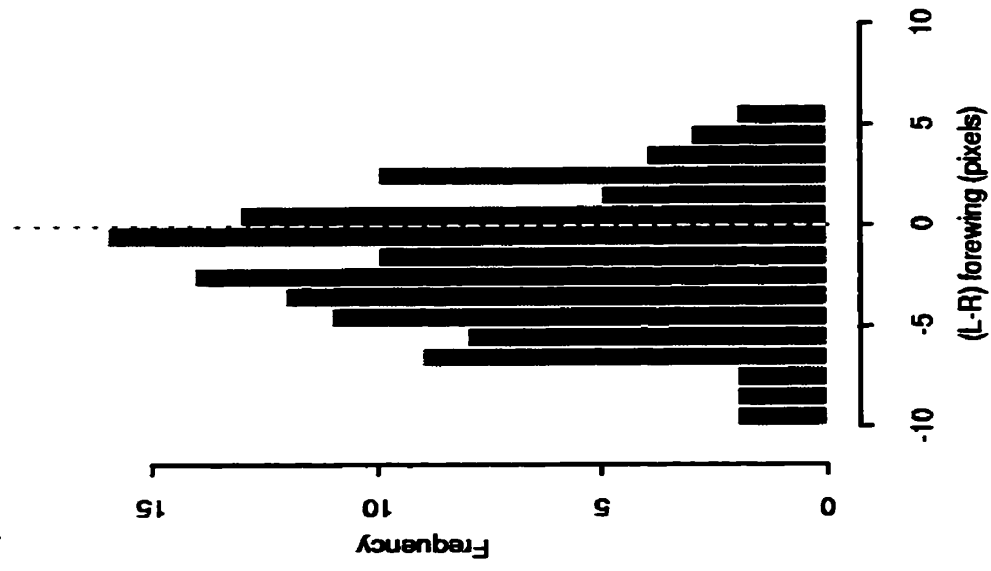
(B) All females



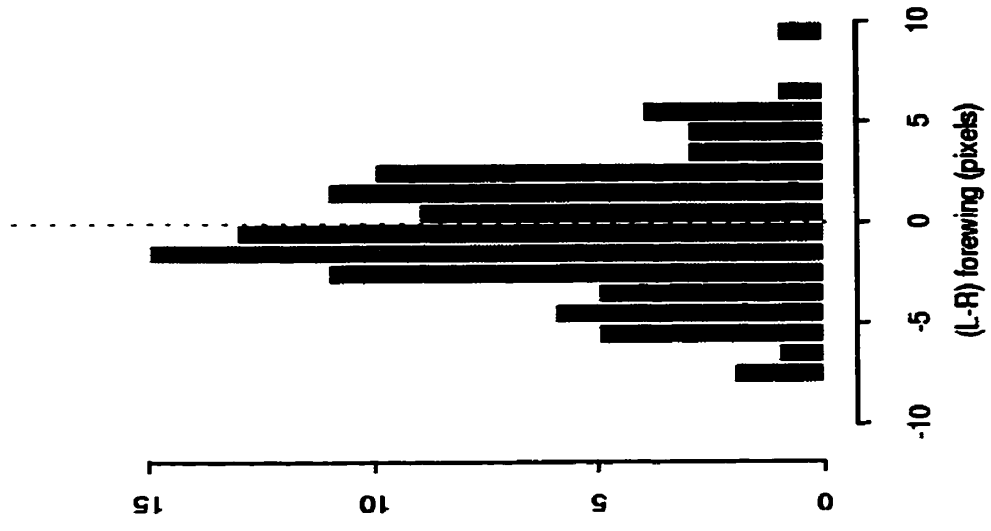
Average femur length (pixels)

**Figure 3-5.** Histograms of signed forewing lengths in all (A) male *C. maculata* and (B) female *C. maculata*.

(A) All males

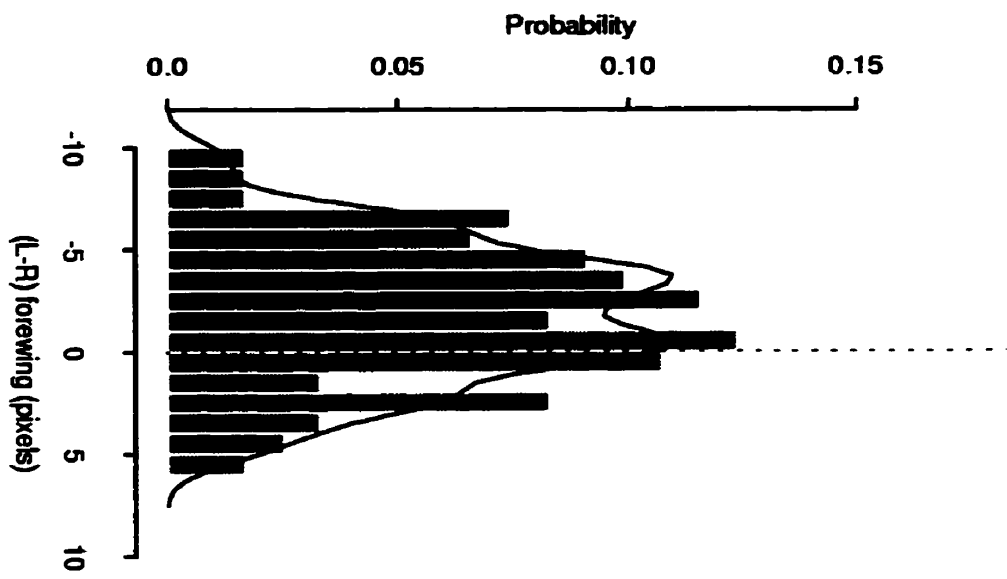


(B) All females

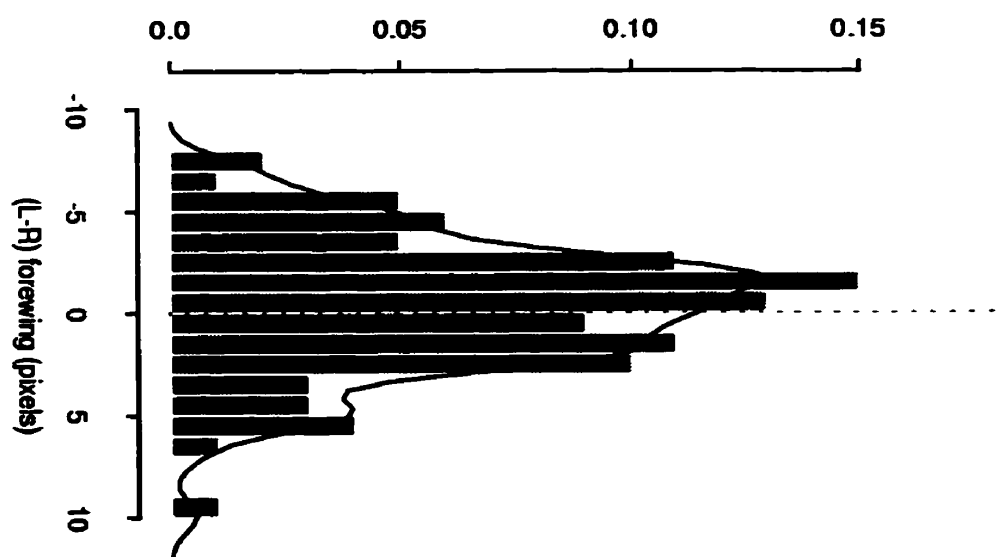


**Figure 3-6.** Probability density plots of signed forewing lengths in all (A) male *C. maculata* and (B) female *C. maculata*. Lines are density smoothing curves.

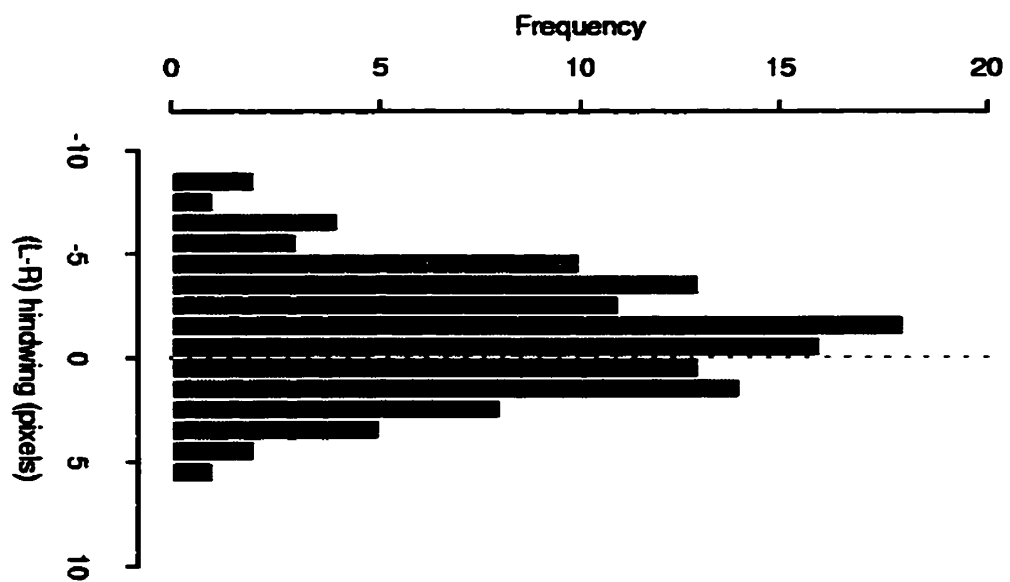
(A) All males



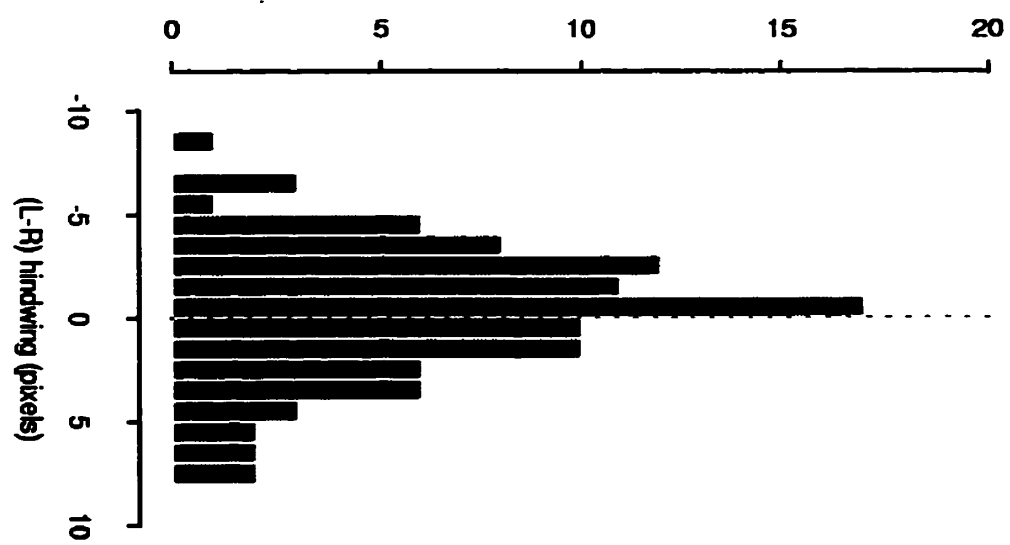
(B) All females



**Figure 3-7.** Histograms of signed hindwing lengths in all  
(A) male *C. maculata* and (B) female *C. maculata*.



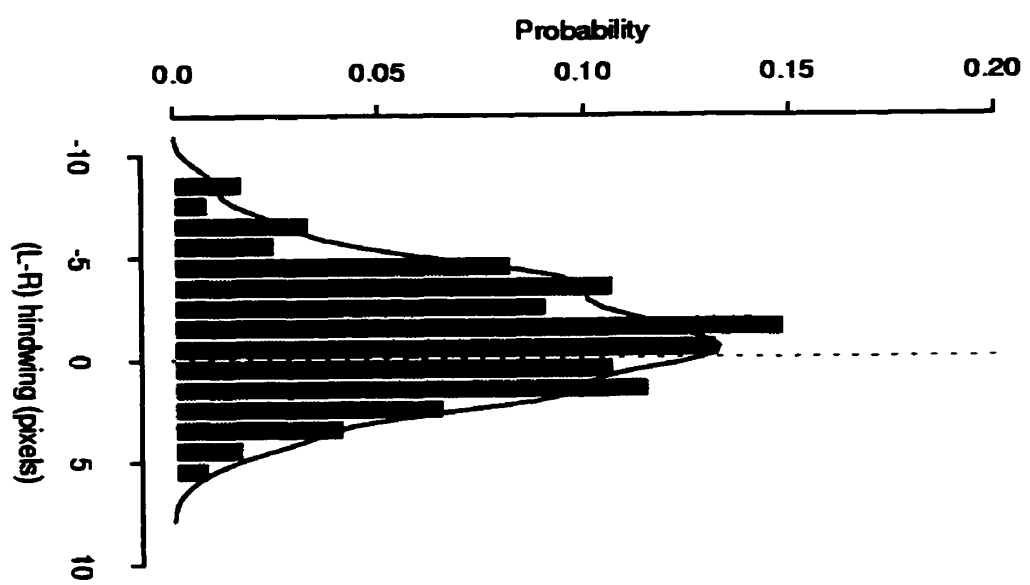
(A) All males



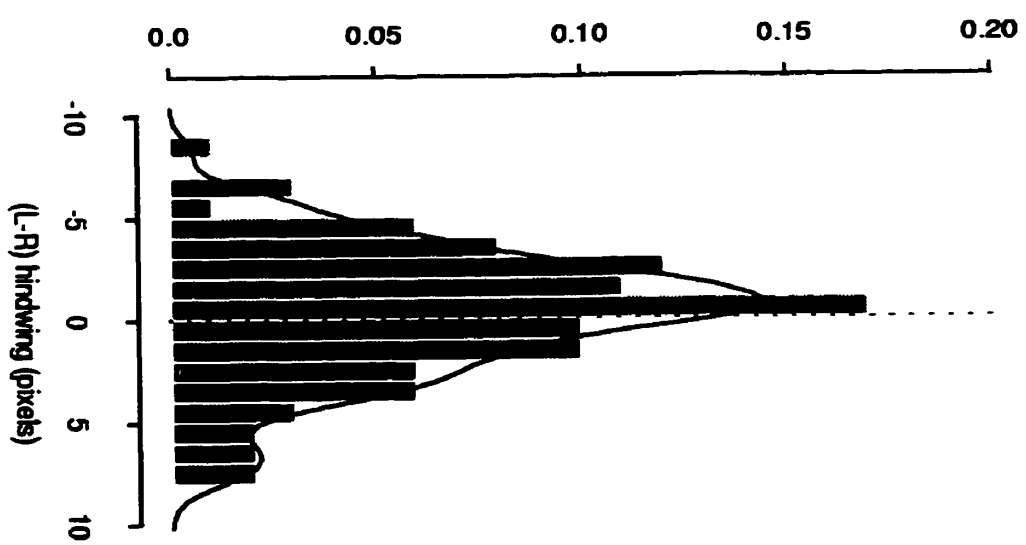
(B) All females

**Figure 3-8.** Probability density plots of signed hindwing lengths in all (A) male *C. maculata* and (B) female *C. maculata*. Lines are density smoothing curves.



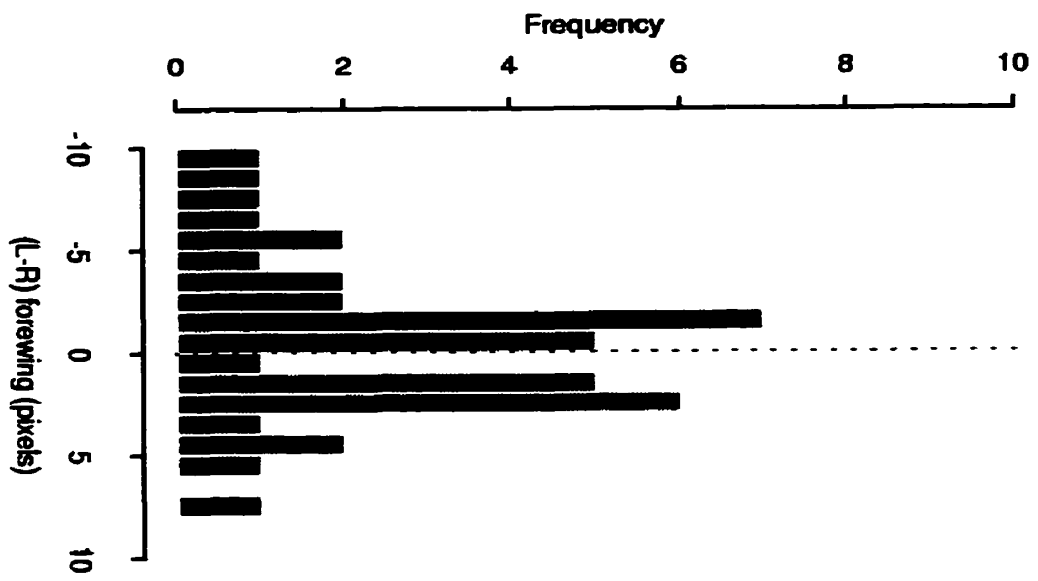


(A) All males

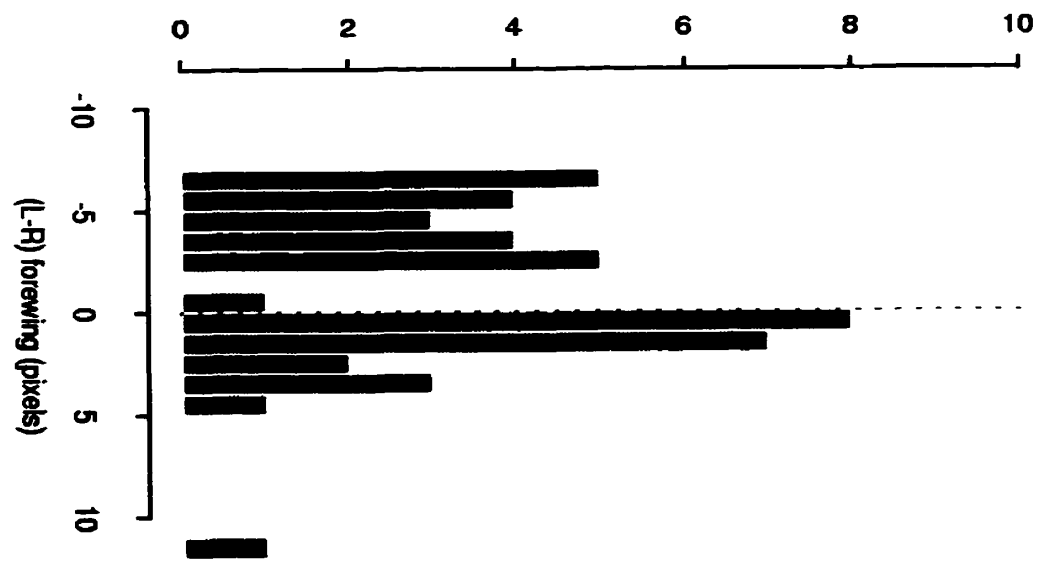


(B) All females

**Figure 3-9.** Histograms of signed forewing lengths in all (A) male *C. aequabilis* and (B) female *C. aequabilis*.



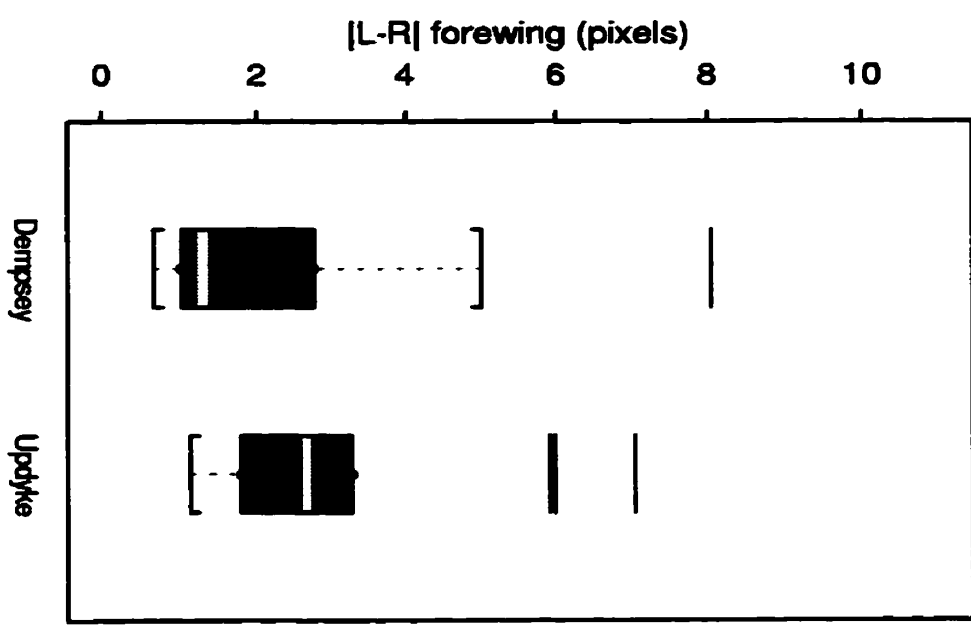
(A) All males



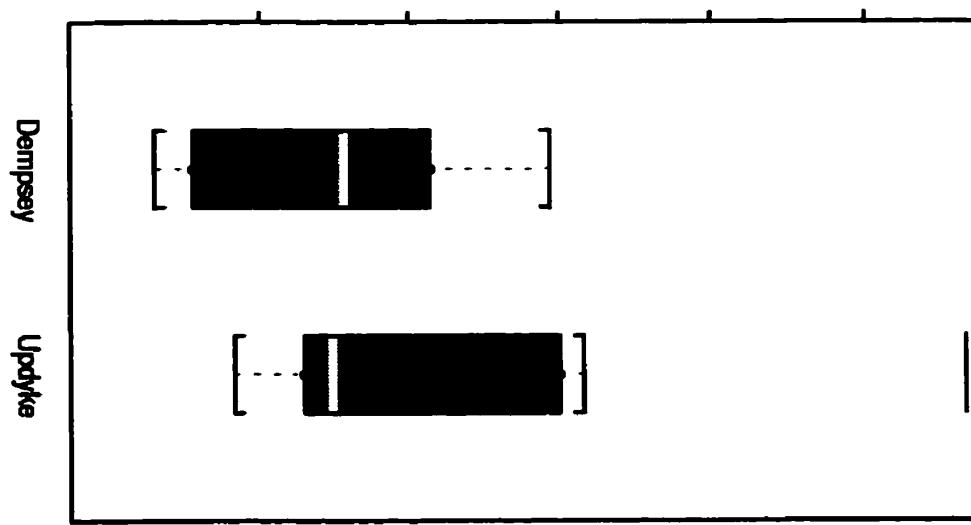
(B) All females

**Figure 3-10.** Boxplots showing median (white bar), interquartile range (box), range (whiskers), and outliers (bars) of mean unsigned forewing asymmetry of (A) subset male *C. aequabilis* and (B) subset females at two pasture landscape sites.

(A) Subset males



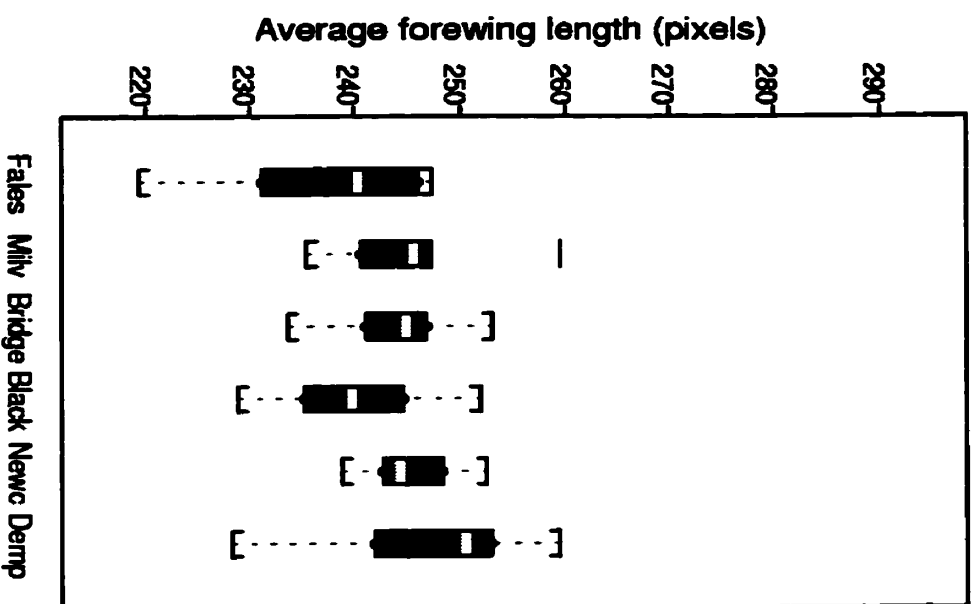
(B) Subset females



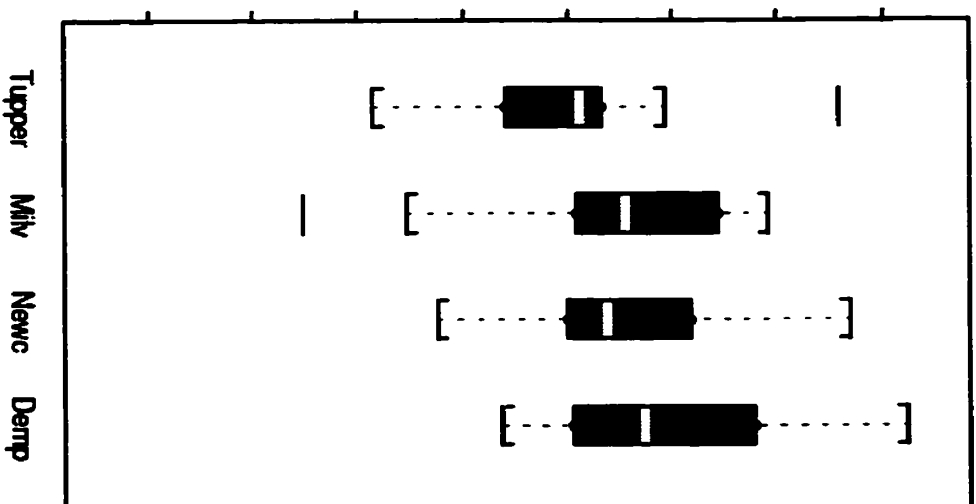
Sampling site

**Figure 3-11.** Boxplots showing median (white bar), interquartile range (box), range (whiskers), and outliers (bars) of mean forewing length of (A) subset male *C. maculata* and (B) subset female *C. maculata* at sites of increasing forest fragmentation.

(A) Subset males



(B) Subset females

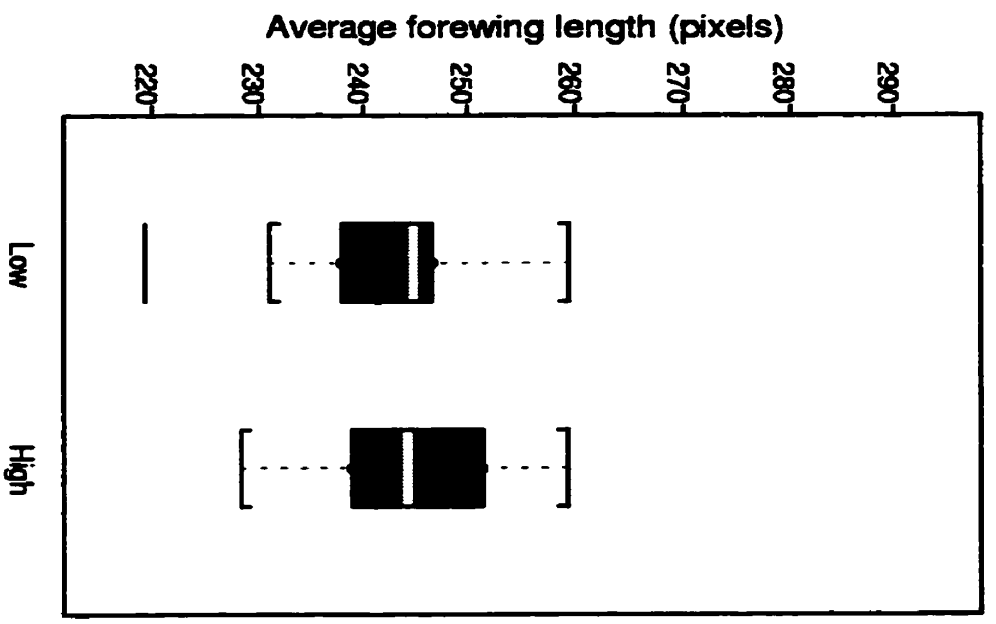


Sampling site

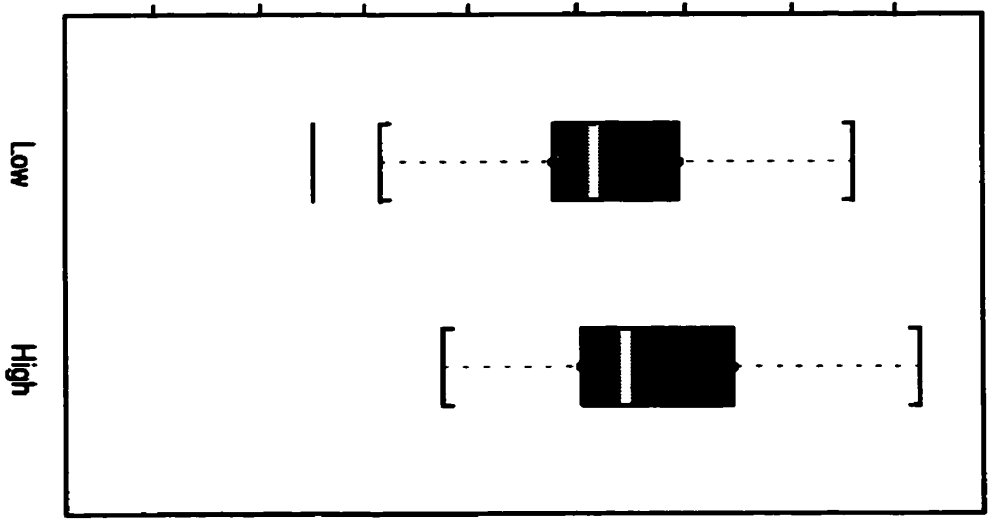
**Figure 3-12.** Boxplots showing median (white bar), interquartile range (box), range (whiskers), and outliers (bars) of mean forewing length of (A) subset male *C. maculata* and (B) subset female *C. maculata* within low and high connectivity landscapes.



(A) Subset males



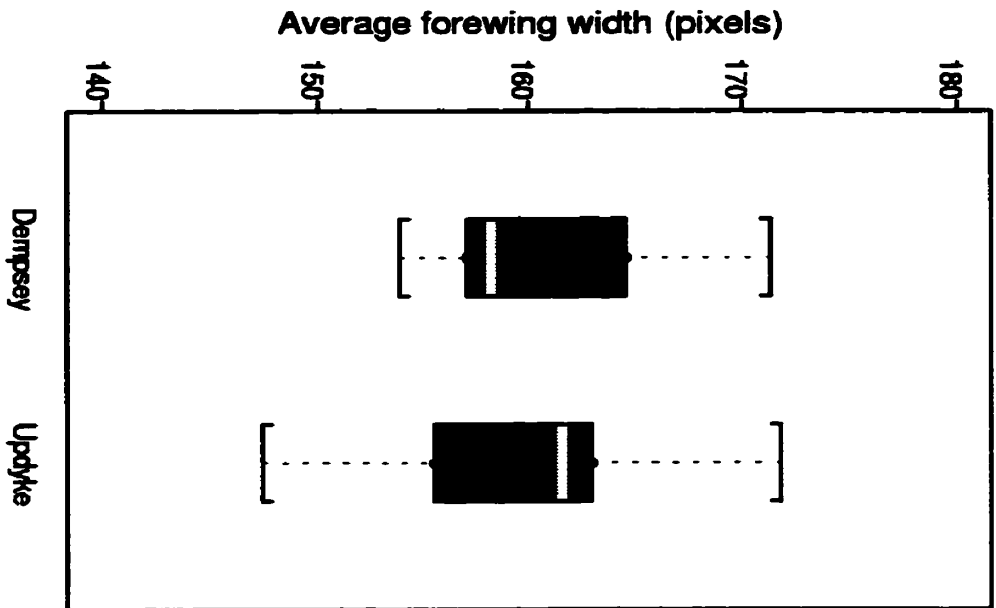
(B) Subset females



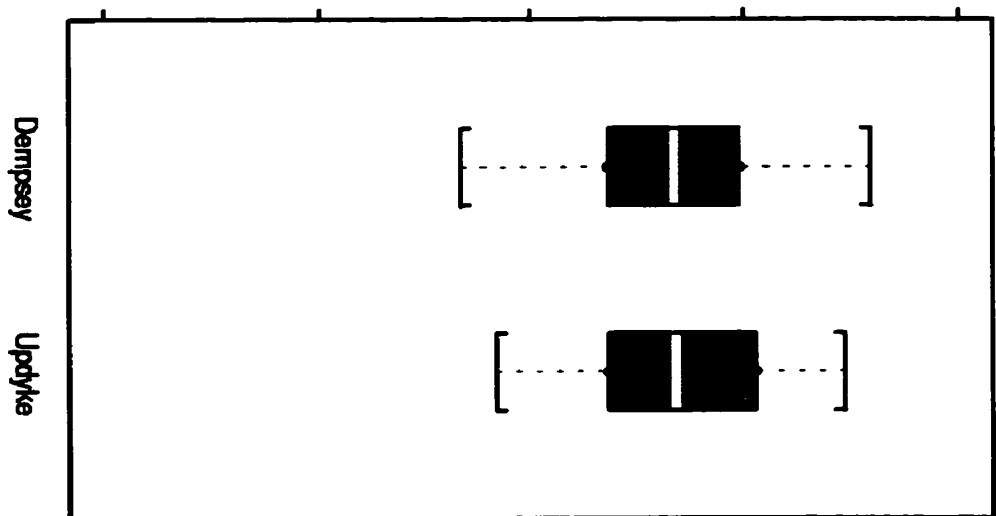
Connectivity

**Figure 3-13.** Boxplots showing median (white bar), interquartile range (box), range (whiskers), and outliers (bars) of mean forewing width of (A) subset male *C. aequabilis* and (B) subset females at two pasture landscape sites.

(A) Subset males



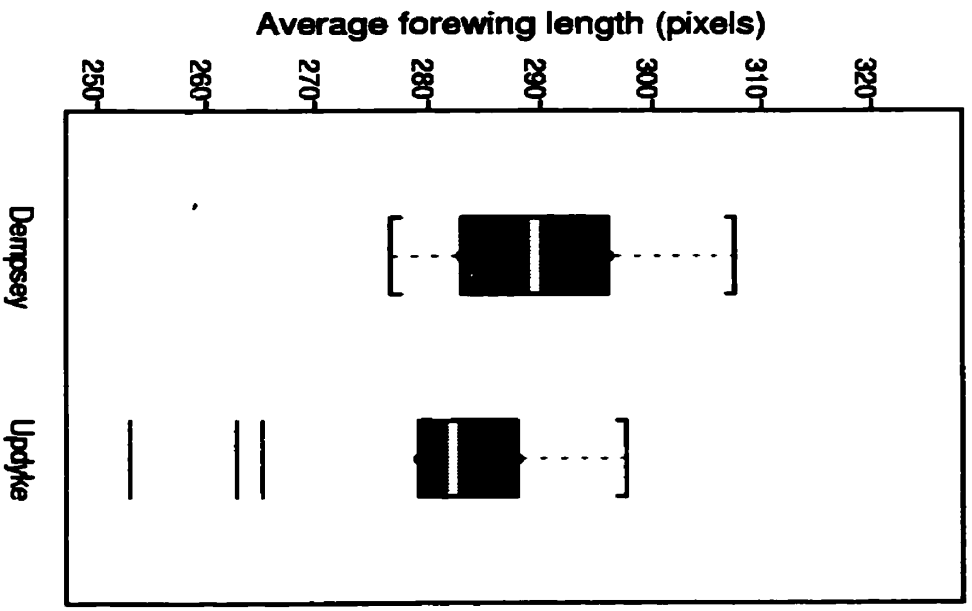
(B) Subset females



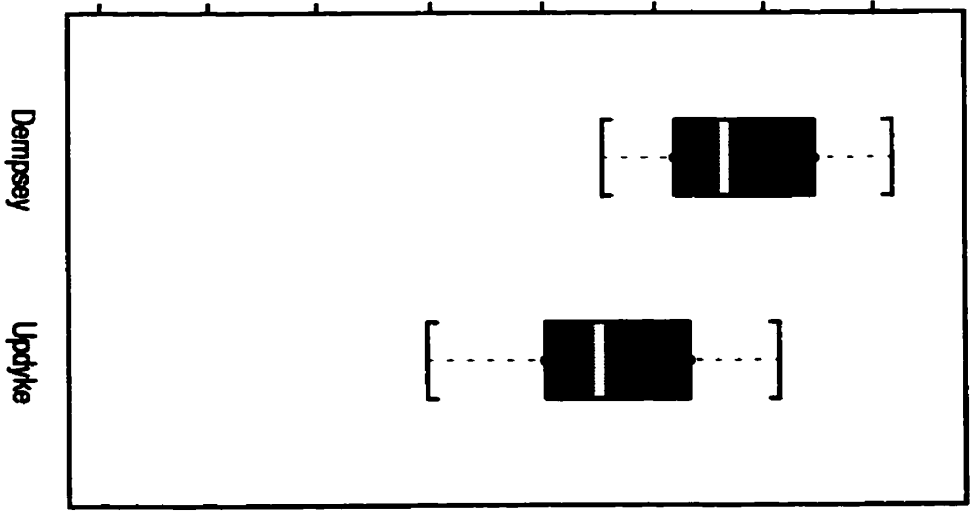
Sampling site

**Figure 3-14.** Boxplots showing median (white bar), interquartile range (box), range (whiskers), and outliers (bars) of mean forewing length of (A) subset male *C. aequabilis* and (B) subset females at two pasture landscape sites.

(A) Subset males



(B) Subset females



Sampling site

## General Discussion

Using surveys I demonstrate that small-scale (measured over metres) and medium-scale (measured over tens to hundreds of metres) characteristics of the landscape are related to stream occupancy by *Calopteryx maculata* and *C. aequabilis*. I show that the small-scale habitat characteristic of amount of sunlight (reaching the transect) changes in importance to *C. maculata* from one summer to the next, and that these changes are consistent with weather conditions. In the relatively cool, cloudy summer of 1996, *C. maculata* - considered a shade-tolerant species (Johnson, 1962; Waage, 1972) - occurred at fewer shaded sites than in 1995. *C. aequabilis* shows a preference for sites open to sunlight in both years. In 1995, when the spring was relatively warm and dry, both *C. maculata* and *C. aequabilis* showed a preference for deep streams. In 1996, when heavy rainfalls occurred several times through the summer, depth was not as important a characteristic in patterns of stream occupancy by either species.

The way in which weather seems to interact with habitat occupancy by these species suggests that it is a potentially significant exogenous factor governing their temporal and spatial distributions. Both species are only active during relatively warm weather, so the number of sunlight hours and the daytime temperatures are likely direct limiting factors on behavior. As a consequence, their population dynamics are likely influenced by weather: if weather is severely limiting in one year (i.e. very cold), the number of mating interactions would likely be reduced, and recruitment in the subsequent year(s) would decrease. Similar effects of weather have been observed elsewhere. For example, Solbreck (1995) tracked the patchy distribution and abundance of lygaeid bugs through time, and found a strong interaction between weather, the behavior of the bugs (flight) and the quality of the host plant (seed production).

Stream occupancy in relation to the medium-scale characteristic of distance to forest

remained consistent for both species over the two years. During my surveys *C. aequabilis* was rarely encountered at forested streams. *C. maculata* - previously considered a forest species (Johnson, 1962; Waage, 1972), occupied sites in a range of forest proximities. I have observed both species making movements between forest and streams that are separated by upwards of 500m of non-resource (pasture) matrix. This behavior is more common to *C. maculata* than to *C. aequabilis*. At sites where forest is further than ca. 500m away, both species remain at the stream throughout the day, and evidently do not use forest as a resource. These observations suggest that *C. maculata* uses forest as a resource more consistently than *C. aequabilis*, but that the latter species does use forest under some circumstances.

Observations also suggest that there is some "threshold" distance at which the costs associated with accessing those distant forest resources outweigh the benefits. These costs may be associated with the energetics of increased movement (e.g. Anholt, 1990; Marden and Rollins, 1994), increased exposure to predation (e.g. Anholt and Werner, 1995), or in relation to lost time in reproductive behavior. The region supports enough occupied heterogeneous landscapes that one could attempt to identify this "threshold" distance. One approach may lie in using wing morphology as an indicator of foraging behavior. For instance, I show that the forewings of *C. aequabilis* individuals inhabiting one such highly fragmented landscape were significantly shorter than those inhabiting a moderately fragmented landscape. I also show that the forewings of female *C. maculata* individuals are slightly longer in moderately fragmented landscapes than in forested landscapes. Taylor and Merriam (1995) show a similar relationship elsewhere. If one could measure individuals from sites with different proximities to forest, the patterns of wing size could be used to infer foraging behavior, and thus locate that "threshold" distance. I see some signs of a beginning to a pattern in my male *C. maculata* specimens, where wing sizes increase with increasing distance to forest, up to a moderately fragmented landscape. My

data do not provide for an assessment beyond this point in the trend.

Ultimately, these relationships between foraging strategies and inter-resource distance are of most concern if individuals, and thus populations, are being detrimentally affected in some way. Are populations inhabiting highly fragmented streams less successful than those where forest is available as a resource? Do these particular aspects of landscape structure affect individual fitness in some way? Previous work (Taylor, 1993) showed that gut contents were not related in a consistent fashion to landscape structure, and that thoracic mass - one indicator of fitness (e.g. Marden and Waage, 1990) - was also more variable among sites within pasture landscapes than among forest and pasture landscapes (Taylor and Merriam, 1995). I examined the degree of fluctuating asymmetry - a possible indicator of stress - in the forewings of *C. aequabilis* individuals collected from a highly fragmented landscape and those collected from a moderately fragmented landscape. I did not find true FA (Palmer and Strobeck, 1986) in either group of individuals, and so could not assess "stress" per se. Nonetheless, I did find that those individuals from the highly fragmented landscape were significantly more asymmetrical than those from the moderately fragmented landscape.

The relationships between the foraging strategies of these damselflies and landscape structure have implications for regional population dynamics. Observations here and elsewhere (Taylor, 1993), suggest that the potential for individuals to disperse (i.e. movement resulting in a reproductive event) over land is influenced by the location of foraging habitat with respect to stream habitat. Moderately fragmented landscapes promote an expansion of the damselflies' extent (sensu Kotliar and Wiens, 1990), and thus may promote more inter-population movements by individuals. An important question to ask, however, is how capable are these species of moving over landscape-scale distances across land, and do these abilities depend on landscape structure?

I answer this question using manipulative experiments. Others have demonstrated that



residency time within a particular landscape element (and thus its connectivity) is contingent upon that element's suitability as a resource (Bach, 1984; Crist *et al.*, 1992; Bennett *et al.*, 1994). I hypothesized that the connectivity of pasture landscapes would be higher than forest landscapes for both species, but that the difference would be more pronounced for *C. maculata*, which uses forest as a resource more consistently than *C. aequabilis*. My hypothesis was supported in part. *C. aequabilis* individuals moved similarly through forest and pasture landscapes, while *C. maculata* moved less readily through forest landscapes. More replicate experiments (higher power) may have been required to detect effects for *C. aequabilis*. I can say with confidence that *C. maculata* individuals inhabiting pasture landscapes are more capable of moving (over land) between populations in those locales than their forest-inhabiting counterparts. I can say with somewhat less confidence that *C. aequabilis* can move equally well over these distances through either matrix type.

I do not know how landscape-scale movements differ along streams in each type of landscape. Movement patterns at the stream have been studied at relatively small spatial scales, always in relation to reproductive behavior or density dependence (e.g. Waage, 1971; Henderson and Herman, 1984; Waage, 1987; Conrad and Herman, 1990; Meek and Herman, 1990). Others have noted that males without territories will often get "bumped along" by territorial males, such that movement rates are relatively high, but net displacements often remain low (Henderson and Herman, 1984; Conrad and Herman, 1990). Females tend to be relatively vagile at these scales (Conrad and Herman, 1987). It would be interesting to perform connectivity experiments at landscape scales along streams of varying oviposition resource densities. In this case, instead of foraging resources (i.e. forest) providing the motivation for damselflies to reside longer, it would likely be the more obligate reproductive resources (i.e. oviposition material) providing the motivation. An effective design including manipulation of both individuals

(displacements) and habitat (oviposition resources) could reveal the propensities of these animals to disperse along streams under different conditions of resource and con-specific densities. In conjunction with my results from Chapter 2, such an experiment would provide a more complete picture of landscape connectivity.

The results I present here describing habitat occupancy and landscape connectivity could be applied in models that predict larger scale processes such as regional distributions. By knowing what small-scale factors govern stream habitat occupancy, and by knowing the propensity of individuals to move in relation to meso-scale landscape structure (i.e. juxtaposition of forests and streams), extrapolations of large-scale distributions can be made (Turner *et al.*, 1989). Such models could be applied to novel areas (using a geographical information system), and tested against survey results. I suggest that, with the benefit of the empirical data that I present describing the details of individual - landscape structure relationships, the predictive accuracy of these models would be relatively high.

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